Ecological impacts of a new invasive species in UK rivers the quagga mussel, Dreissena rostriformis bugensis (bivalva: dreissenidae; Andrusov 1897)

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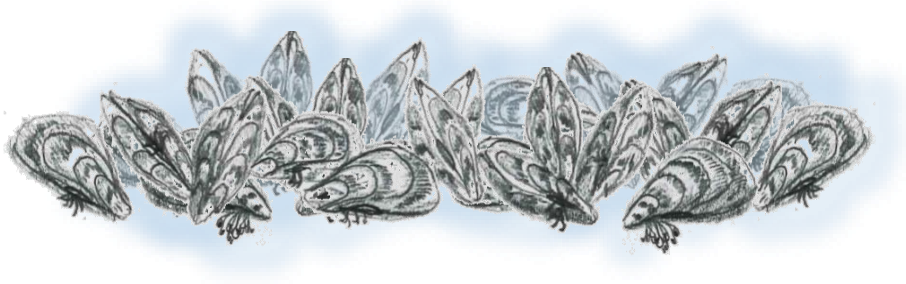
ECOLOGICAL IMPACTS OF A NEW INVASIVE SPECIES IN UK RIVERS: THE QUAGGA MUSSEL, DREISSENA ROSTRIFORMIS BUGENSIS (BIVALVA: DREISSENIDAE; ANDRUSOV 1897)



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I, **Daniel Nash Mills**, confirm that the research included within this thesis is my own work or that where it has been carried out in collaboration with, or supported by others, that this is duly acknowledged below, and my contribution indicated. Previously published material is also acknowledged below.

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Details of collaborations:

1. The author is indebted to the geography department of Loughborough Univeirsty for use of a laboratory flume facility in their Rivers Laboratory alongside significant advice and tutelage from the head of department Professor Steven Rice and laboratory manager Dr. Richard Harland. Experiments described in chapter 4 could not have been achieved otherwise.

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Project Summary

The primary objective of this project was to conduct quantitative investigations on impacts of non-native 'quagga mussel,' *Dreissena rostriformis bugensis* in the UK range. A freshwater bivalve mollusc from the Ponto Caspian region, the quagga mussel was considered, prior to first record, a threatening invasive species to UK biodiversity. Given lack of regional knowledge regarding the influence of *D. r. bugensis* on native ecology, quantitative research into observable and potential impacts of the species was considered important.

Following a general introduction and statement of project aims, this dissertation was divided into three parts. Part 1, titled 'observable impacts,' comprised two data chapters; each explored influences of *D. r. bugensis* on invertebrate communities *in situ*. The first chapter presented an annual-scale benthic survey to compare invertebrate communities between invaded and uninvaded lotic reaches within the UK range. The second described benthos colonisation experiments testing the influence of mussel shells at higher densities than found at the time.

Part 2 was titled 'impact mechanisms' and contained three chapters. The first presented results from laboratory flume experiments to assess geomorphic impacts of *D. r. bugensis* in rivers. The second chapter provided extended discussion on the impacts of suspension feeding *Dreissena* spp. in rivers, incorporating a series of *ex situ* and *in situ* experiments on *D. r. bugensis* in the the UK invaded range. The third chapter was derived following first record of invasive shrimp *Dikerogammarus haemobaphes* within the *D. r. bugensis* range. Possible commensalism between *Dreissena* spp. and other Ponto Caspian species was investigated in the context of Invasional Meltdown Hypothesis (Simberloff and Von Holle 1999).

Part 3 of the dissertation, titled 'likelihood of impacts,' included two final chapters. The first aimed to assess the preferred habitats of *D. r. bugensis* within the known invaded range. Additionally, this work analysed change in reach-scale mussel densities since the annual-term survey of part 1. Further, discussing whether other regional environments could be at risk of future invasion. The final dissertation chapter contained a summary of project conclusions with synthesis of all findings to comment on potential impacts of *D. r. bugensis* in the invasive range and other UK freshwaters.

Acknowledgments

I have many friends and collegues to thank for helping me construct this dissertation.

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Table of Contents

Part 3: Likelihood of Impact

List of Figures

List of Tables

Chapter 1: *Introduction*

Establishment of species in regions outside their native range has followed anthropogenic breakdowns of biogeographic barriers (Karatayev et al., 2003; Ricciardi 2003; Crowl et al., 2008). Introductions, both accidental and deliberate (Smith et al. 1999; Early et al. 2016), may perturb natural evolutionary pathways (Vermeij 1996; Mooney and Cleland 2001; Simberloff 2013) and with increasing recorded frequency (Lowe et al. 2004; Lockwood et al. 2005) constitute a phenomenon unique in the history of the planet (Elton 1958). Due to their impacts on native communities, invasive taxa have been considered a risk to global species biodiversity second only to habitat destruction (Bellard et al. 2016). Control or eradication of many invasive species may be impossible to achieve (Pimentel et al., 2000; Ricciardi et al., 2011) and if human technological and diplomatic progress eventually addresses issues of ongoing anthropogenic habitat destruction and climate change (see: Travis 2002; Thomas et al. 2004; Brook et al. 2008); biological invasions may provide the longest-lasting legacy of our era. One increasingly referred to as the Anthropocene (*sensu* Crutzen 2002; Steffen et al. 2007; Lewis and Maslin 2015).

Following the seminal work of Elton on biological invasions (Elton 1958), impacts of non-native species have received increased academic and public attention (Pfeiffer & Voeks 2008; Francis & Chadwick, 2013). Non-native taxa may be better adapted than cohabiting natives to compete for energy, water and space resources (Williamson and Fitter 1996; Sakai et al. 2001; Diham et al. 2005). Likewise, they may perform better under predation or disease pressure (Alderman et al. 1990; Kobak et al. 2014) with greater plasticity for surviving environmental extremes (Stachowicz et al. 2002; Tyrrell and Byers 2007) and anthropogenic habitat destruction (Byers 2002*a*; Didham et al. 2007). Such advantages can facilitate introduced species, allowing them to become successful in recipient environments (Holway and Suarez 1999; Stohlgren and Schnase 2006).

Following establishment, studies have frequently recorded displacement of native organisms with similar ecological function (Herbold and Moyle 1986; Huxel 1999; Mooney and Cleland 2001), changes in trophic energy transfers (Chapin et al. 1997; Hogan et al. 2007) and adoption of niche roles (see: Hutchinson 1978) previously absent in the recipient region (Simberloff 1995). Where introduced species cause deleterious or detrimental impacts to native taxa, they may normally be termed 'invasive' rather than simply 'non-native' or 'alien' (CBD 2008; Blackburn et al. 2011). According to the United Nations Convention on Biological Diversity (2008), the definition of an invasive species is: 'non-native species that threaten ecosystems, habitats or species' (CBD 2008). In some cases, invasive species have caused broader shifts to an alternative, stable environmental state, triggering alteration to community function (Mack and D'Antonio 1998; Sanders et al. 2002; Blackburn et al. 2014).

Since Elton (1958), high profile species invasions have been documented across the globe. These include the zebra mussel *Dreissena polymorpha* (Pallas 1771) in North America (Mills et al. 1993*a*; Ricciardi and MacIsaac 2000), Nile perch *Lates niloticus* (Linnaeus 1758) in central Africa (Ogutu-Ohwayo and Hecky 1991; Pringle 2005), grey squirrel *Sciurus carolinensis* (Gmelin 1788) in Western Europe (Bertolino and Genovesi 2003; Gurnell et al. 2004) and European rat *Rattus* spp. in Australasia and the Pacific (Holdaway 1996; Towns and Broome 2003). However, rate of introduction has not been equal geographically (Meyerson and Mooney 2007; Early et al. 2016), being more frequently recorded in the industrialised global north and small tropical islands (Early et al. 2016; Turbelin et al., 2016). Recipient regions have been associated with human trading activity (Meyerson and Mooney 2007; Hulme 2009), European colonial histories (Crosby 1986; McNeeley 2006) and biogeographic isolation (Simberloff 1995; Mooney and Cleland 2001). Countries such as the United Kingdom, with a long tradition in maritime trade and globalism, have both exported and received a particularly high number of species invasions (Keller at al. 2009; Gallardo and Aldridge 2013*a*), despite

recent progress with biosecurity protocols for import goods and aquatic recreational activities (Beninde et al. 2015; Tollington et al. 2017).

The impacts of invasive species establishment can be highly varied across environmental conditions (Peterson 2003; Jiménez-Valverde et al. 2011) with both direct and indirect influences on native taxa (Rodriguez 2006; Preston et al. 2012). For example, predatory invasive lionfish *Pterois volitans* (Linnaeus 1758) in the Caribbean (Arias-González et al. 2011; Albins and Hixon 2013) domestic cat *Felis catus* (Linnaeus 1758) on Pacific Islands (Medina et al. 2011; Medina et al. 2014) and rats *Rattus* spp. in Australasia (Mulder et al. 2009; Towns and Broome 2003) not only reduced native prey populations, but caused cascade effects on other trophic groups that were particularly strong in more isolated ecological communities. Elsewhere, establishments of invasive plants *Lantana camara* (Linnaeus 1758) in Austrailia and *Bromus tectorum* (Linnaeus 1758) in North America have outcompeted growth of native flora, restructuring plant communities to favour shrubland over forest. In warm summer conditions, these changes have significantly increased forest fire incidence (Knapp 1996; Brooks et al. 2001; Berry et al. 2011). In a notable UK example, invasive crayfish *Pacifastacus linesculus* (Dana 1852) were linked to direct predatory impacts on native equivalents (Manchester and Bullock 2001; Bubb 2006) but found to cause greater deleterious effects as vectors for non-native parasite *Aphanomyces astaci*, to which native crayfish were highly susceptible (Holdich et al. 2003; Holdich et al. 2009). UK rivers, highly interconnected by industrial canal networks (Gallardo and Aldridge 2013*b*), facilitated dispersal of a resultant 'crayfish plague' (Alderman et al. 1990; Holdich and Reeve 1991), associated with the loss of most native UK crayfish populations from 1970-1997 (Holdich et al. 1999). While not all species introductions result in such deleterious impacts on native ecology (Colautti and MacIsaac 2004; Rodriguez 2006), predicting whether newly established taxa could be similarly damaging has been considered a key goal of invasion biology (Parker et al. 1999; Crooks 2002

Strayer et al. 2006). With greater knowledge of impact risks from suspected invasive species, environmental authorities may justify resource allocation for control and mitigation (Byers et al. 2002*b*).

Invasive species that are considered to be 'ecosystem engineers' have been of particular concern in recent years (Jones et al., 1994; Gergs 2003; Gutierezz et al. 2003). These taxa may alter the physical structure and biological resources of invaded environments (Jones et al., 1994; Crooks 2002; Karatayev et al., 2002), influencing habitability for cohabiting organisms (Jones et al. 1997) with cascading impacts on community structure and function (Stewart & Haynes 1994; Mitchell et al., 1995; Gutierezz et al. 2003) alongside damage to human infrastructure (Sousa et al. 2009). Examples from the terrestrial environment may include the North American beaver *Castor canadensis* (Kuhl 1820) in Chile, shown to significantly reduce forest canopy coverage near rivers (Anderson et al. 2005), in turn affording spatial opportunities for the establishment of invasive herbaceous taxa (Rozzi et al. 2004). Alternatively, the Eurasian salt cedar *Tamarix* spp. in Central America, with deep roots and high evapotranspiration potential, may reduce water tables to unsustainable levels for native plants (Crooks 2002; Shafroth et al. 2005). In aquatic environments, seasonal dieback of the macrophyte *Phragmites australis* (Cavanilles 1799; European variant) in North America has been shown to dramatically increase bankside litter layers, altering the diversity and density of cohabiting macrofauna (Farnsworth 1999; Talley et al. 2001). Further, invasive animals such as the Chinese mitten crab *Eriocheir sinensis* (Milne-Edwards 1853) and American Signal Crayfish (Dana 1852) have been shown to destabilise benthic substrates through burrowing (Herborg et al. 2003; Crawford et al. 2006; Holdich et al. 2014); increasing stream turbidity (Johnson et al. 2010; Harvey et al. 2014), recirculating benthic nutrients (Stenroth and Nyström 2003) and potentially reducing river bank stability (Rudnick et al. 2005; Faller at al. 2016; Rice et al. 2016). Generally, the impacts of invasive 'ecosystem engineers' may be more varied

compared to other invasive species and may influence a broader range of cohabiting ecology (Crooks 2002).

A frequently cited ecosystem engineer, the Ponto-Caspian bivalve mollusc *Dreissena polymorpha* (Pallas 1771), has become highly widespread in UK freshwaters (Aldridge et al. 2004; Gallardo and Aldridge 2013b). Named colloquially the 'zebra mussel', *D. polymorpha* has been found for over 150 years across the lowlands of England and Wales (Minchin et al. 2003; Aldridge et al., 2004), colonising a diverse range of lentic and riverine systems (Elliot et al. 2005; Lucy et al. 2007). Unlike most UK bivalves, *D. polymorpha* is epifaunal rather than burrowing (Kryger and Riisgård 1988; Baker 1997), with keratinous byssus attachment to the bed (Mackie 1991; Eckroat 1993) and a mobile veliger larval stage (MacIsaac et al. 1992; Johnson 1995); each a typical characteristic of marine molluscs (Ackerman et al. 1994; Orlova 2002). Outside the UK, establishment of *D. polymorpha* has often been accompanied by the 'quagga mussel', a closely related species *Dreissena rostriformis bugensis* (Andrusov 1897; **Figure 1.1**). This includes in freshwater environments of Eastern Europe (Karatayev et al. 1997; Zhulidov et al. 2010), Western Europe (Molloy et al. 2007; Bij de Vaate and Beisel 2011), the North American Great Lakes (Mills et al. 1996; Roe et al. 1997) and South West Interior (Grigorovich et al. 2008; Nalepa 2010). The widespread distribution of *Dreissena* spp. compliments broad environmental tolerances (McMahon 1996; Quinn et al. 2013), physical robustness to predation (Kobak et al. 2010; Zu Ermgassen and Aldridge 2011), niche flexibility (Mackie 1991; Morton 1993), generalistic feeding (MacIsaac 1996; Strayer 1999) and high reproductive capacity (Sprung 1993; Ram et al. 2011). These traits, deemed common across other invasive species (Sakai et al. 2001), have been used to explain the rapid development of high-density benthic populations of *Dreissena* spp. where introduced (Mackie 1991; McMahon 1996).

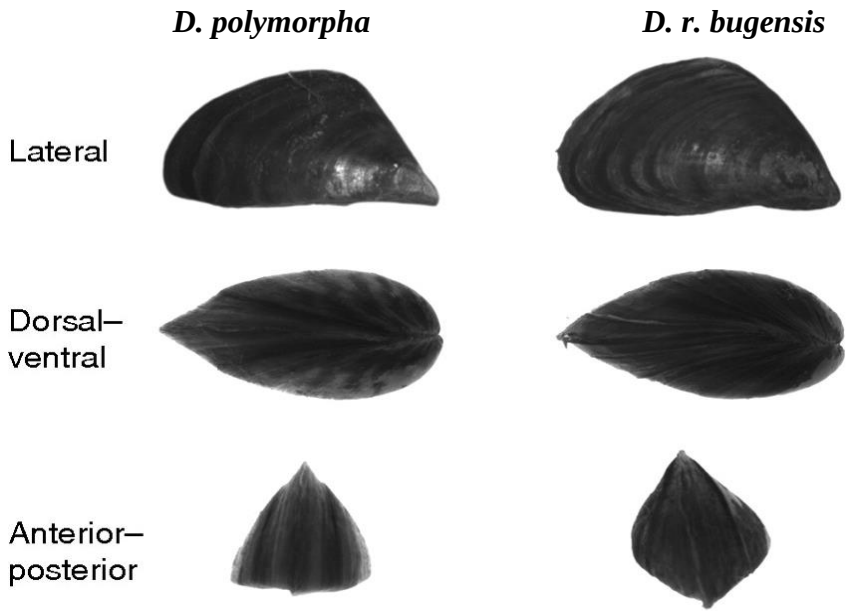


Figure 1.1 Comparison of *Dreissena polymorpha* and *Dreissena rostriformis bugensis* (adapted from: Peyer et al., 2011).

While *D. polymorpha* impacts on cohabiting ecology have not been widely studied in the UK (Aldridge et al. 2004); their invasion of the North American Great Lakes (first record 1988; Herbert et al. 1989), alongside that of *Deissena rostriformis bugensis* (first record 1991; May and Marsden 1992), presented significant impacts on aquatic ecology (MacIsaac et al. 1992; Stewart et al. 1994; Ricciardi et al. 1998 Vanderploeg et al. 2002). For example, mussel suspension feeding was widely associated with reduction of phytoplankton (MacIsaac 1996; Makarewicz et al. 1999), zooplankton (MacIsaac et al. 1991; Wong et al. 2003), protozoans (Cotner et al. 1995; Finday et al. 1998) and total suspended loads (Strayer et al. 1999; Budd 2001) in North American lentic systems. Rejected food materials, emitted as pseudofacaes, may settle and concentrate on lake beds, enriching substrate nutrient concentrations (Botts et al. 1996; Roditi et al. 1997), altering food resources for macrophytes, biofilm and certain benthic invertebrates (Lowe and Pilsbury 1995; Gergs et al. 2011; Ward and Ricciardi 2007).

However, the physical impact from *Dreissena* spp. shells (of both live and dead mussels) has been considered the most important driver of change to community structure across many

invaded environments (Botts et al. 1996; Ward and Ricciardi 2007). To particular benefit of benthic macroinvertebrates where hard substrate is limited (Stewart et al. 1998; Beekey et al. 2004); studies have shown shells increase substrate surface area (Ricciardi et al. 1997; Stewart et al. 1999) and as a result, enhanced predator (González and Downing 1999; Mayer et al. 2001) and flow refugia (Ricciardi 1997). Further, *Dreissena* spp. facilitation of algal biofilm and bacterial communities suited to hard substrates may provide additional food sources for grazing invertebrate and fish taxa (Kobak et al. 2013; Higgins and Zanden 2010). Finally, shells may provide suitable substrate for further *D. polymorpha* larval settlement (Herbert et al. 1991; Martin Mörtl 2003); demonstrating a form of intraspecies facilitatation contributory to the formation of high-density mussel beds (also termed druses).

For example, the North American Great lakes, have presented mussel bed densities of 16,400 individuals m^{-2} in Lake Michigan (Nalepa et al. 2009), 75, 000 m^{-2} in Lake Huron (Nalepa et al. 1995) and 342, 000 in Lake Michigan (Nalepa et al. 2009) with similar numbers found in European freshwaters; including 13, 400m^{-2} in Germany's Lake Plön, 7000m^{-2} in Poland's Lake Beloslawskie (Ramcharan et al. 1991) and 1000m^{-2} in Lakes IJsselmer and Lake Markermeer (1991). In such cases, benthic substrates may be covered by both live and dead *Dreissena* spp. shells (Stewart et al. 1998), deleteriously swamping native bivalves (Ricciardi et al. 1995; Ricciardi et al. 1998; Sousa et al. 2011) and potentially triggering benthic anoxia due to intense respiration pressures (Caraco et al. 2000; Effler et al. 2004). Such impacts may place rarely occurring taxa of conservation importance under threat in invaded environments (Ricciardi et al. 1998).

Indeed, generally facilitative impacts of *Dreissena* spp. found for benthic ecology (Stewart et al. 1998; Ward and Ricciardi 2007) should not be misconstrued as necessarily positive. Invertebrate communities, while found at higher density post *Dreissena* spp. invasion, have typically presented reduced community evenness (Ricciardi et al. 1997; Ward and Ricciardi

2007). Further, *D. r. bugensis* may facilitate the arrival of other invasive invertebrates (Gallardo & Aldridge 2013*a*; Gallardo & Aldridge, 2015). For example, invasive, predatory amphipods of *Dikerogammarus* spp. have shown particular affinity to *Dreissena* spp. shells (Kobak & Żytkowicz, 2007) and like other taxa may benefit from increased habitat complexity provided by mussel beds (Gallardo & Aldridge, 2013*a*). Other authors have suggested *Dreissena* spp. are pioneer invasives under Invasional Meltdown Hypthesis (*sensu* Simberloff and Von Holle 1999) with commensal relationships complimenting the establishment of other non-native taxa, particularly from the same evolutionary range (e.g. Gallardo and Aldrige 2015).

Given such widespread potential impacts, the first UK record of a second *Dreissena* species, *D. r. bugensis*, was of significant concern for environmental authorities in October 2014 (See: Aldridge 2014). *D. r. bugensis* was named as the most damaging potential UK invasive species just months prior to its discovery (Roy et al. 2014), due to its high likelihood of arrival, establishment and damage to native biodiversity by 2024. While holding similar traits to the already established *D. polymorpha* (Quinn et al. 2013), it was thought *D. r. bugensis* could be more prolific in UK freshwaters given invasion histories elsewhere (Aldridge et al. 2014). *D. r. bugensis* exhibits greater tolerance for food limitation (Baldwin et al. 2002) increasing temperatures (Quinn et al. 2013) and water column depth (Mills et al. 1996); appearing to gradually displace *D. polymorpha* as the dominant *Dreissena* species in various lentic (Mills et al. 1993*b*; Wilson et al. 2006) and lotic (Mills et al. 1996; Ricciardi and Whoriskey 2004) systems in North America and Europe. Moreover, *Dreissena* spp. had been shown to exhibit boom-bust population dynamics in invaded environments (Ramcharan et al. 1992; Burlakova et al. 2006); meaning the newly arrived variant could be more prolific than the cousin already long-present in the UK.

Problematically, predicting ecological impacts of a newly established invasive species can be difficult (Williamson 1999; Roy et al. 2014). Invasion dynamics may be significantly varied

across both geographic space (Lodge et al. 1998; Peterson 2003; Kulhanek et al. 2011*a*) and time (Crooks and Soulé,1999; Seebens et al. 2017). Notably, the majority of supporting study on *Dreissena* spp. impacts had been in large, interconnected lentic systems of North America's Great Lakes during the late 20th century (Lucy et al. 2008). In such regions, environmental conditions, cohabitating native ecology and anthropogenic pressures are very different to those found in the UK; rendering direct comparisons likely inappropriate.

Exacerbating this issue, the site of first record for *D. r. bugensis* in the UK was a short reach of the Wraysbury River (<2km^{-1} length); a small (<5m wide), gravel-bed stream near Heathrow Airport in west London (Lat 51.45225; Long -0.520528; Aldridge 2014; **Figure 1.1**). Very little research had been undertaken on *Dreissena* spp. impacts in river environments (Lucy et al. 2008) and where found, examples were largely conducted in rivers such as the Hudson (Caraco et al. 1997; Strayer et al. 1999), Oswego (Effler and Siegfried 1998) and Seneca (Effler and Siegfreid 1994; Effler et al. 2004) of North America. Here, *Dreissena* spp. had been thought to favour deep, wide, low velocity streams (Strayer et al. 1996) or canal systems (Aldridge 2014). Subsequent studies had supported this, showing reduced *Dreissena* spp. feeding efficiency with stream flows >0.2m s^{-1} (Ackerman 1999), larval intolerance to ultraviolet light penetration in shallow waters (Seaver et al. 2009; Thaw et al. 2014) and increased susceptibility to visual predation by water fowl (Petrie and Knapton 1999). Given such factors, establishment of *D. r. bugensis* in Wraysbury River was considered surprising (Aldridge et al. 2014).

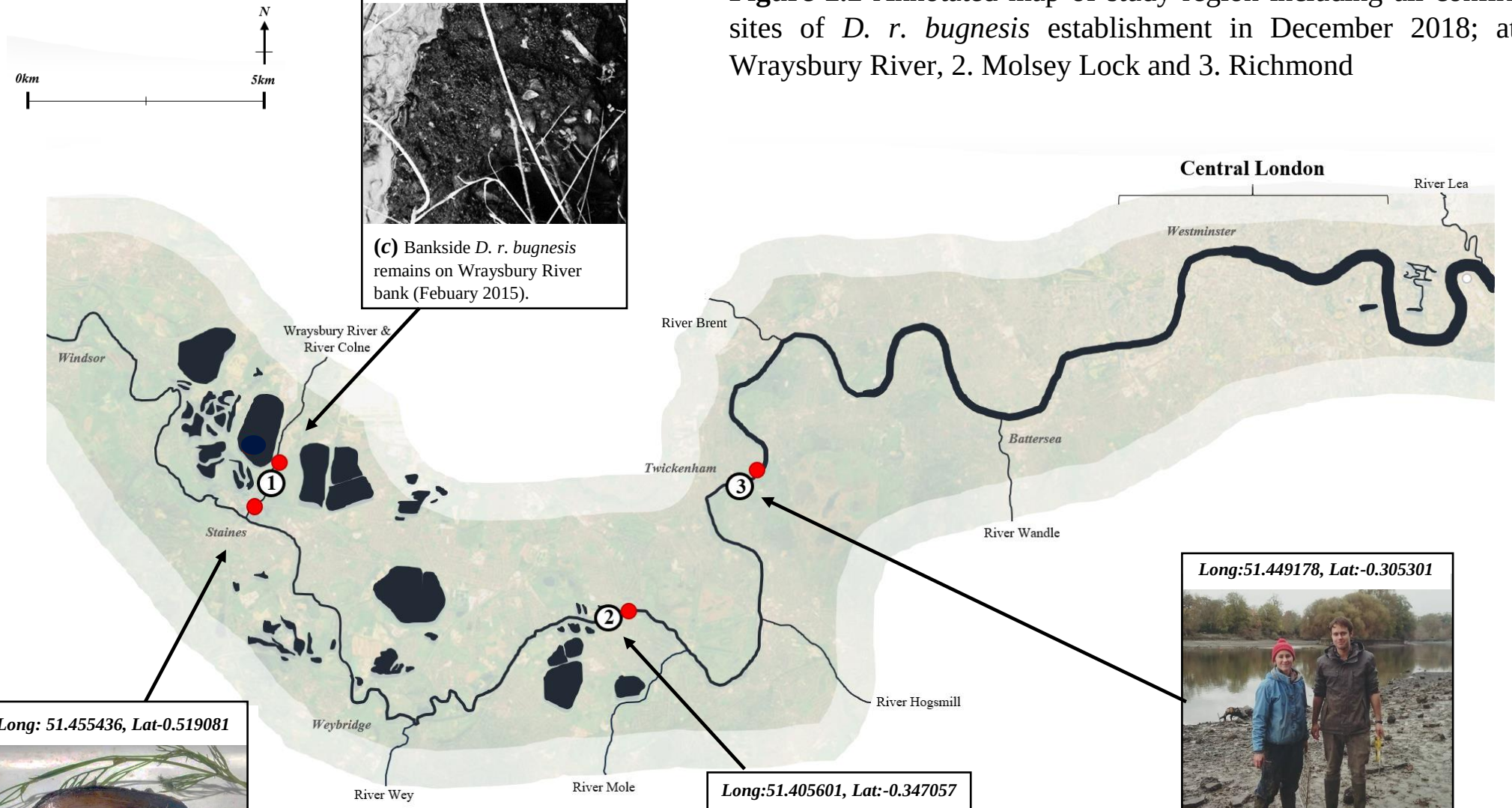
At the outset of this project, it was considered whether establishment in Wraysbury River pointed to greater than expected habitat flexibility of *D. r. bugensis* and/or boom dynamics of an early-invasion period (*sensu* Simberloff and Gibbons 2004). Certainly, the UK invasion of *D. r. bugensis* had appeared to commence in earnest. During the time frame of the study alone (2014-2018), the known range of *D. r. bugensis* appeared to expand at least ~30 km^{-1}

downstream from the point of first record to Richmond on Thames (Lat 51.449178; Long -0.305301; **Figure 1.2a**). A series of overt interactions with cohabiting ecology were also found, albeit anecdotally. These included *D. r. bugensis* fouling of native Unionidae spp. (**Figure 1.2b**), evidence of *D. r. bugensis* predation by terrestrial mammals (**Figure 1.2c**) and (alongside invasive *D. polymorpha* and Asiatic Clam *Corbicula fluminea* (Müller 1774) blockage of an Environment Agency eel pass at Molsey lock, West London (Lat 51.405545; Long -0.347190; **Figure 2d**). Despite such observations, work to scientifically elucidate such issues was required. The principle aim of this thesis was to conduct investigations on the ecological impacts of *D. r. bugensis* establishment in UK rivers.

Thesis Structure

For this dissertation, comprising 6 main chapters: a holistic range of current and potential *D. r. bugensis* impacts were investigated; each drawing directly on primary observations from either the Wraysbury River (Lat 51.45225; Long -0.520528), other sites in the Thames catchment and one further location in the Norfolk Broads, eastern England (Long: 52.739205, Lat: 1.497049). The first section, titled '*Part 1. Observed Impacts*' comprised two study chapters designed to test *in situ* for observable influences of *D. r. bugensis* on macroinvertebrate benthos. The first, Chapter 2 of this dissertation, described investigations of an annual survey (May 2015 - 2016) comparing community structure across a range of invaded and uninvaded sites in the Wraysbury River. Chapter three built on this to experimentally test macroinvertebrate responses at higher *D. r. bugensis* bed densities than found in the aforementioned survey. Both chapters provided benchmarks as the first quantitative field studies to assess impacts of *D. r. bugensis* on benthic communities in a UK stream.

Figure 2.2 Annotated map of study region including all confirmed sites of *D. r. bugnesis* establishment in December 2018; at 1. Wraysbury River, 2. Molsey Lock and 3. Richmond



(*c*) Bankside *D. r. bugnesis* remains on Wraysbury River bank (Febuary 2015).

(*d*) Native *Unio* spp. fouled by *D. r. bugnesis* collected in Wraysbury River. (August 2015)

(*b*) *D. r. bugnesis* inside Molsey eel pass, River Thames (May 2016).

(*a*) Volunteers on ZSL citizen science benthic surveys, River Thames (November 2017).

All photos property of the author

The second phase of the project, titled '*Part 2. Impact mechanisms'* comprised three chapters designed to examine a series of *D. r. bugensis* traits. Each was hypothesised to impact benthic ecology following guidance from available literature on *Dreissena* spp. and field observations in the Thames catchment. For example, Chapter 4 described experimental investigations into geomorphic impacts of *D. r. bugensis* byssus attachments to river substrate. Following this, chapter 5 examined potential impacts of *D. r. bugensis* suspension feeding in riverine environments. Finally, Chapter 6 investigated the possible commensalism between *D. r. bugensis* and other invasive species. Discussed in the context of Invasional Meltdown Hypothesis (Simberloff and Von Holle 1999), this latter work was inspired by the discovery of invasive shrimp *Dikerogammarus haemobaphes* (Eichwald 1841) in Wraysbury River (during summer 2017).

Across both parts 1 and 2 of this study, investigations were conducted to create knowledge and better inform discussion on the potential of *D. r. bugensis* to impact ecology in UK freshwaters. Considering progress made in chapters 2-6, a final phase of study was completed, titled: '*Part 3. Likelihood of impacts*.' This section drew on repeated indications from previous chapters mussel density would be positively related to the magnitude of *D. r. bugensis* ecological impacts; with similar findings for literature elsewhere (e.g. Burlakova et al. 2000; Barbiero and Tuchman 2004; Ward and Ricciardi 2007). An initial study (Chapter 7) examined *D. r. bugensis* habitat preferences within the invaded UK range. This was conducted to assess which lotic habitats, if any, were most likely to present mussel densities required for significant ecological impacts in future. An extended, discussion (Chapter 8) developed conclusions made in this chapter and synthesised all study findings. The conceptual diagram of the study can be seen in **Figure 1.3** (overleaf) and despite linkages shown, each chapter was designed as a self-contained unit, able to be read independently of others. This was to facilitate future publication opportunities for this work.

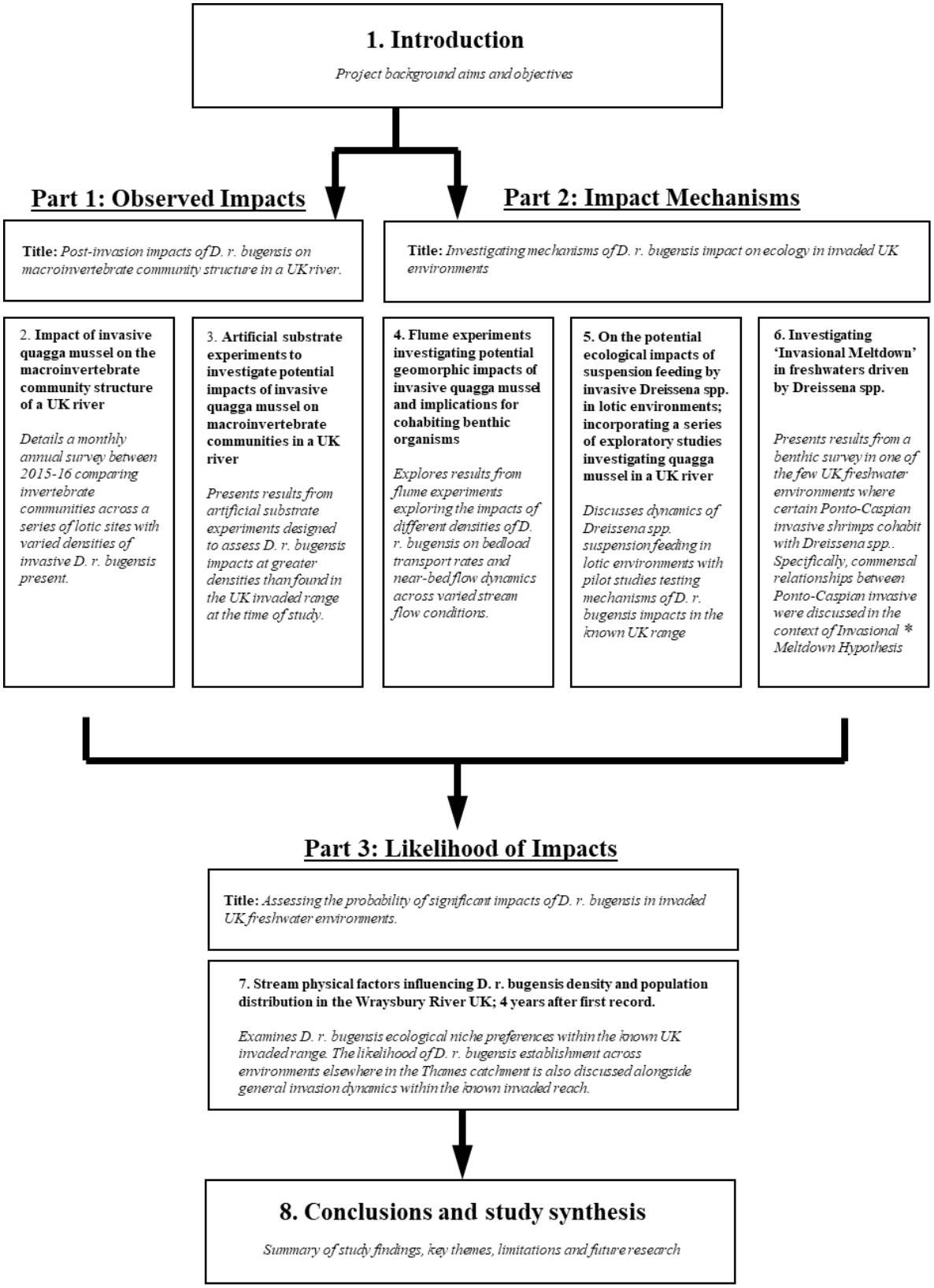


Figure 1.3 Schematic of thesis structure.

The project outlined intended to provide quantitative primary research on current and potential ecological impacts of *D. r. bugensis* in UK rivers. Similar work has been called for following species introductions for *D. polymorpha* in North America (Herbert et al. 1989) and Ireland (Minchin et al. 2005) alongside bloody-red mysid *Hemimysis anomala* (Sars 1907) in France, ferret *Mustela furo* (Linnaeus 1758) in the Spanish Canary Islands (Medina and Martín 2010), little fire ant *Wasmannia auropunctata* (Roger 1863) in Israel (Vonshak et al. 2010), Gambian rat *Cricetomys gambianus* (Waterhouse 1840) in North America (Perry et al. 2006) and killer shrimp *Dikerogammarus villosus* in the UK (Sowinsky 1984; MacNeil et al. 2010), among others. Without research on newly arriving invasive species, an episode of natural history, even if but a footnote, would be lost.

Specifically, early invasion dynamics of several non-native fauna in UK freshwaters have received limited scientific attention. For example, the zebra mussel *D. polymorpha*, New Zealand mud snail *Potamopyrgus antipodarum* (Gray 1843; Heyward and Edwards 1962), North American shrimp *Gammarus tigrinus* (Sexton 1939; Platvoet et al. 2009*a*) and the Ponto-Caspian shrimps *Crangonyx pseudogacilis* and *Cheliocorophium curvispinum* (Wijnhoven et al. 2011) have each become established in the UK without study to describe their impacts at the point of invasion. As such, little knowledge exists of what native taxa, if any, were displaced from their respective niche in the invaded range. It was hoped this project would 'buck this trend' to ensure more knowledge was available for *D. r. bugensis*; considered at outset the most potentially threatening invasive to UK biodiversity (Roy et al. 2014).

Part 1: Observed Impacts

Post-invasion impacts of D. r. bugensis on macroinvertebrate community structure in a UK river.

Chapter 2: Impact of invasive quagga mussel (*Dreissena rostriformis bugensis*, Bivalva: Dreissenidae) on the macroinvertebrate community structure of a UK river

Summary:

The arrival of invasive quagga mussel (*Dreissena rostriformis bugensis*) to the UK necessitates rapid study to evaluate its impact on benthic community structure where colonisation has occurred. In the Wraysbury River (west London), impact on benthic invertebrate community structure by invasion of quagga mussel was measured by comparing a series of invaded and uninvaded study sites over an annual period of monthly sampling. It was apparent that despite quagga mussel consistently forming a large proportion of stream biomass in invaded sites, community taxon richness and composition did not vary significantly in comparison to uninvaded sites. Similarly, total community biomass and density when excluding quagga mussel was mostly homogeneous across the study reach; with the exception of one site with the highest quagga mussel biomass and density. If quagga mussel biomass and density increased over time to levels found at this site, more significant changes to native community structure might be expected. This study represents a first benchmark for understanding the progression and impacts of quagga mussel invasion in UK rivers and these results will be essential for comparison in evaluating future change and impacts.

Publication note for chapter:

The following study was published as a research article (Mills et al. 2017), full reference:

Mills DN, Chadwick MA, Francis RA (2017) Impact of invasive quagga mussel (*Dreissena rostriformis bugensis*, Bivalva: Dreissenidae) on the macroinvertebrate community structure of a UK river. *Aquatic Invasions* 12(4): 509-521

Accordant to Kings College London rules on theses incorporating publication, work is presented as for the accepted article; except reference listings which have been collated with others for this dissertation (from 213 pp.).

Introduction

The structure of freshwater communities throughout the world is altered by the colonisation of non-native species (Strayer 2010; Błońska et al. 2015). While some alien taxa appear to cause little deleterious change to native communities, others are invasive and can cause significant reductions in native biodiversity and impact ecosystem processes (Parker et al. 1999; Francis and Chadwick 2012). In the United Kingdom and other European countries, various taxa-specific studies provide a range of evidence for such impacts (e.g. Alderman et al. 1990; Aldridge et al. 2004; Gherardi and Acquistapace 2007; Sousa et al. 2011). Further, invasive species are receiving increasing attention from both competent authorities and the public (Pfeiffer and Voeks 2008; Francis and Chadwick 2012). Rising awareness of the monetary cost associated with biotic invasions also drives concern (Elliot et al. 2005; Williams et al. 2010), expanding the need for study on high impact species.

Several freshwater invasives have recently been ranked for the UK by their potential to invade and diminish biodiversity (Roy et al. 2014). These include the bivalve mollusc *Dreissena rostriformis bugensis* (Andrusov 1897), widely known as the 'quagga mussel.' In September 2014, this species was confirmed for the first time in the UK in the Wraysbury River, a small tributary of the River Thames in west London (Aldridge et al. 2014).

A native of the Ponto-Caspian region, quagga mussel is a close relative of *Dreissena polymorpha* (Pallas 1771), the 'zebra mussel'. Dreissenid mussels rapidly colonise lentic systems (Karatayev et al. 2015), typically contributing a large proportion of total benthic invertebrate biomass (e.g. Dermott and Kerec 1997; Stewart and Haynes 1994; Burlakova et al. 2005). As physically robust (Czarnołęski et al. 2006; Kobak et al. 2010) and highly fecund (Mackie 1991; Closs et al. 2004), *Dreissena* spp. often form dense colonies of over 1000 individuals m^{-2} on the benthic littoral (Mackie 1991; Ricciardi et al. 1997; Strayer et al. 1999).

Such environments have been very well studied: *Dreissena* spp. in lakes may act as efficient filter feeders (Hecky et al. 2004; Vanderploeg et al. 2010), removing plankton, bacteria and suspended silt from the water column. This shifts native taxa biomass from the pelagic to benthic zones (Stewart and Haynes 1994).

Quantitative observation of *Dreissena* spp. impacts in rivers is less frequent than in lakes. However, studies in various environments consistently suggest colonization may alter invertebrate habitat availability (Stewart and Haynes 1994; Botts et al 1996; Kuhns and Berg 1999; Beekey et al. 2004); swamp the shells of native Unionid mussels (Nalepa 1994; Ricciardi et al. 1998; Sousa et al 2011); and consume seston, thereby reducing phytoplankton abundance and limiting other filter feeding invertebrates and pelagic feeding species including certain fish (Jack and Thorp 2000; Fuentes 2003). Further, *Dreissena* spp. presence in interconnected rivers could facilitate the establishment of other Ponto-Caspian invaders that hold evolutionary traits adapted for cohabitation (Kobak et al. 2014; Gallardo and Aldridge 2014). Field-based evidence for such relationships are currently limited; however in laboratory experiments, the Ponto-Caspian shrimp *Dikerogammarus villosus* (Sowinsky 1894) utilised *Dreissena* spp. beds as refugia from predation more effectively than *Gammarus fossarum* (Koch 1835), a western European counterpart (Kobak et al. 2014).

The potential for quagga mussel colonisation to cause such facilitative effects for either invasive or native species in rivers is uncertain. In lakes, *Dreissena* spp. beds are known to provide both complex habitat and refugia for other invertebrate species to flourish (Stewart et al. 1998; Bailly and MacIsaac 2000; Ricciardi 2001; Burlakova et al. 2012). They have also been considered as a bioremediation tool for regulating algal blooms, improving water clarity and encouraging macrophyte settlement (Stybel et al. 2009; McLaughlan and Aldridge 2013). In many cases, *Dreissena* spp. colonies have been associated with marked increases in native

invertebrate richness and biomass (Higgins and Vander Zanden 2010; Karatayev et al. 2015); however little comparative work has been done for lotic systems.

Uncertainty and limited study of *Dreissena* spp. colonisation impacts on community structure in rivers highlight the need for further observation. Within the UK, this is particularly pressing in the case of quagga mussel because it has been ranked as the most threatening potential invasive species to UK biodiversity (Roy et al. 2014). The colonisation of quagga mussel to the Wraysbury River (Aldridge et al. 2014) allows for a timely study to evaluate invertebrate community structure in a newly colonised lotic system. The objective of this study was to assess the impact of quagga mussel on invertebrate community structure by comparing a series of localised invaded and uninvaded sites along the Wraysbury River.

Methodology

Study Area

Quagga mussel was first found in the UK in the Wraysbury River by the UK Environment Agency (Aldridge 2014). Situated near Staines-upon-Thames (western London), this stream is a shallow (<0.5m depth) and relatively short (c. 8.7km) branch of the River Colne system, a tributary of the River Thames. The catchment is Devensian gravels and the river is dominated by a sandy gravel/pebble substrate. At the study reach the stream has a homogeneous width (approximately 4-5m) and is predominantly characterised by laminar, glide flow. Land use is varied throughout the catchment and local features include an area of protected pastoral moorland, multiple navigational canals, patches of suburban housing and a section of the London orbital motorway. Seasonal records collected by the UK Environment Agency between January 2014 and December 2016 give mean nutrient concentrations for the Wraysbury River as total oxidised nitrogen 9.4 N mg L^{-1}, and orthophosphate 0.3 mg L^{-1} (EA, pers. com. 2017).

A nearby reservoir (Wraysbury Reservoir) is of particular note. Quagga mussel in the Wraysbury River were found to be restricted downstream of a small, intermittent pumping facility servicing the reservoir (EA, pers. com. 2014). For this study, six approximately equidistant sites were selected downstream of the facility with two additional sites located upstream (**Figure 2.1**: sites 1-8) along a 1.8km reach.

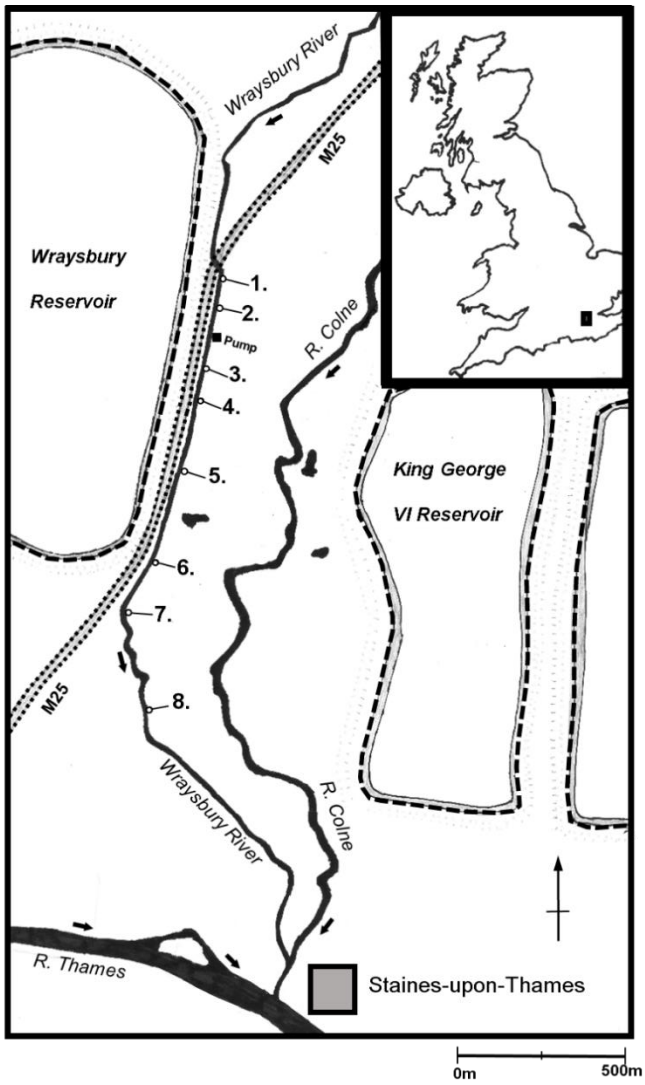


Figure 2.1 Location of the Wraysbury River study reach (~Lat 51.45225; Long -0.520528) and associated study sites (marked 1-8). No quagga mussels were collected at sites 1 & 2 and these sites provide the uninvaded site group. The location of the pump facility between sites 2 & 3 is also marked. See Table 2.1 for coordinates of individual study sites.

The sampling reach in each case was characterised by laminar, glide flow. An initial pilot study in April 2015 confirmed distances between study sites (**Table 2.1**), and that each held similar physical characteristics including mean stream depth and wetted width. Qualitative estimations of substrate typology suggested a homogenous mixture of sand, gravel and pebble throughout the study sites (**Table 2.1**). These parameters did not appear to meaningfully change throughout the annual study period.

Table 2.1 Physical characteristics of study sites (1-8) from an initial pilot study in April 2015. Parameters include stream dimensions, qualitative estimations of substrate typology and study site location coordinates. Mean stream depth (m) was taken for each site by averaging values from three equidistant measurements across the channel, repeated for the most upstream, middle and downstream points of the 25 m^{-2} sampling reach. Mean stream width (m) was taken by averaging measurements of the wetted channel at these same points using a tape measure.

Site Number	**Mean width (m)**	**Mean depth (m)**	**Distance downstream (km)**	**Substrate typology % Estimates**				**Location Coordinates**	
				Silt	*Sand*	*Gravel*	*Pebble*	*Latitude*	*Longitude*
1	5.3	0.32	0	10	40	25	25	51.460444°	-0.516361°
2	4.9	0.38	0.17	15	40	20	25	51.459056°	-0.517389°
3	4.8	0.34	0.54	20	30	20	30	51.455889°	-0.518917°
4	5.2	0.44	0.69	20	30	35	15	51.454556°	-0.519389°
5	4.8	0.34	0.96	10	35	25	30	51.452250°	-0.520528°
6	5	0.36	1.26	15	25	30	30	51.449806°	-0.522361°
7	4.8	0.37	1.44	10	35	25	30	51.448500°	-0.523861°
8	5.2	0.35	1.78	10	20	30	40	51.445722°	-0.523139°

Monthly invertebrate sample collection was undertaken at each study site between May 2015 and May 2016. The sampling reach at each site was $25m^{-2}$ of the wetted channel downstream of the stream entry point. Biological sampling and supporting physicochemical measurements were completed within the last 3 days of each month. Physicochemical measurements, taken to further characterise the Wraysbury River and confirm a reasonable similarity in conditions

between the invaded and uninvaded sections of the river, included stream conductivity (µs cm^{-1}), dissolved oxygen (DO; mg L^{-1}), pH, alkalinity (mg L^{-1}), hardness (mg L^{-1} as $CaCO_3$), temperature (^oC) and flow rate (m s^{-1}). For stream conductivity, DO, pH, and temperature, data was collected on the same day as biological sampling with 5 spot samples per study site using a HACH^{TM} HQ30d multi-probe and HI-9811-5N pH/EC/TDS/^oC portable meter. Alkalinity and hardness were measured with 3 0.5L samples of stream water collected per site, then analysed in the laboratory within 24hours of collection using a HACH^{TM} digital titration kit. Stream flow rate (m s^{-1}) was measured on a quarterly/seasonal basis for each site using a propeller flow meter. Per site, 5 equidistant measurements at 0.6 depth were made throughout the channel width, half way between the top and bottom of the sampling reach.

Benthic Invertebrate Survey

Each month between May 2015 and May 2016, five invertebrate samples were taken at each study site, in a random location within the 25m^{-2} sampling reach, using a Surber sampler (0.33m x 0.33m with a net-mesh size of 250 µm^{-1}). Biological material and sediment was collected to an approximate depth of 2cm into the river substrate. When captured, large pebbles were washed and removed and the remaining sample was collected in 0.5L polyethene pots before preservation with Industrial Methylated Spirit (90%). In the laboratory, all individual specimens were removed from the sample, enumerated and identified under a high power ocular microscope. Identification was made to species level with the exception of *Simulium* spp., Oligochaeta spp., and the family Chironomidae which were identified to tribe. Specimens of Limnephilidae spp. and Hydropsychidae spp. were grouped at family level due to morphological ambiguity at their smallest size-ranges. All specimens were measured for length to the nearest 0.5mm on their *a*-axis.

Data Analysis

For this study, like previous quantitative studies of *Dreissena* spp. establishment (e.g. Stewart et al. 1998; Dermot and Kerec 1997; Bunnell et al. 2009), invertebrate community structure was analysed with emphasis on taxa biomass in addition to density. Biomass composition is generally considered a strong indicator of community structure (Saint-Germain et al. 2007) and is frequently used when summarizing quantitative differences in freshwater invertebrate communities (e.g. Stone and Wallace 1998; Benke and Wallace 2003; Tessier et al. 2008). This approach is advantageous when individuals of different taxa range through several orders of magnitude in body mass, and may better provide a general picture of processes affecting community structure (*sensu* Saint-Germain et al. 2007). The use of biomass also permits assessment of the proportional, physical contribution of different taxa or taxonomic groups to the total benthos (e.g. Leeper and Taylor 1998; Bourassa and Cattaneo 2000; Howard and Cuffey 2006).

First, invertebrate richness and abundance was calculated for each sample. Estimates of total invertebrate biomass per site as dry mass g m^{-2} (herein referred to as biomass, DM g m^{-2}) were then obtained by summing individual biomass of all collected individuals. Biomass per individual was estimated from body size using previously published length-weight regressions (Smock 1980; Marchant and Hynes 1981; Huryn and Wallace 1987; Benke et al. 1999; Baumgartner and Rothhaupt 2003; Stoffels et al. 2003; Edwards et al. 2009). Where conversion parameters were not available for a specific taxa, a published regression for members of the same genus was used in the first instance, or an averaged regression for the respective family or class (**Appendix I**; 268 pp.).

For each monthly dataset, a series of one-way ANOVAs were performed to assess the variability of mean taxa richness, invertebrate density (individuals m^{-2}) and total taxa biomass

per site excluding quagga mussel. When a monthly dataset did not meet assumptions of normality (determined using Shapiro-Wilk), data were natural-log transformed prior to analysis. For mean quagga mussel biomass alone (within invaded sites 3-8 only), monthly datasets did not conform to parametric assumptions even following transformation so one way ANOVA on ranks were used. For all analyses where there was significant variation between site groups, post hoc pairwise comparisons were undertaken using a Tukey test.

Summaries of mean annual invertebrate density, Shannon-Weiner diversity (Magurran 1988; Krebs 1989), taxa richness and total community biomass (excluding quagga mussel) were also made for each site. Furthermore, the % contribution of different invertebrate feeding groups to mean annual biomass was also calculated for each site. Present taxa were assigned feeding groups according to previously published classifications (Mandaville 2002). Such analysis is a common approach when interrogating invertebrate assemblage data (e.g. Troelstrup and Hergenrader 1990; Walters and Post 2011; Cauvy-Fraunié et al 2016), providing further examination of community structure characteristics.

Community ordination analyses were used to further summarize the data set. Mean biomass values (g m^{-2}) per taxa for each site were analysed incorporating all monthly measurements. Data were log(X+1) transformed to moderate for the effects of rare or highly abundant taxa (Clarke and Green 1988; Legendre and Gallagher 2001) and all taxa accounting for less than 0.5% of total mean biomass per month were excluded to reduce distortion of assemblage differences. All analyses were completed using the statistical software package PRIMER-E v.6.1.13; Primer-E Ltd., 2009 (Clarke and Gorley 2006; Clarke 1993; Clarke and Warwick 2001).

Ordinations of community structure were performed using Non-Metric Multidimensional Scaling (NMDS) based on Bray-Curtis dissimilarities. This is a widely used approach for

displaying invertebrate community structure data (e.g Kobayashi and Kagaya 2004; Thomson et al. 2005; Ercoli et al. 2015) and was applied to display between-site differences in mean biomass composition as weighted by taxa present. All monthly data sets were incorporated into the analysis, with 12 data points per site averaged to show the mean annual placement of each site within the plot.

One-Way ANOSIM was then used to assess similarity in mean biomass composition between invaded and uninvaded site groups. Additionally, a similarity of percentages (SIMPER) analysis (Clarke and Warwick 2001) was used to determine the percentage contribution of different invertebrate taxa towards any dissimilarity in biomass composition between site groups. A second SIMPER analysis was then run to assess species contributors to similarity within site groups.

Results

A total of 81642 invertebrate individuals comprising 57 taxa were identified with a mean annual richness of 15 taxa throughout all sites. Quagga mussel was consistently found at sampling locations below the reservoir pump facility (Sites 3-8), where mean annual density was 54 individuals m^{-2}. While nearly all other taxa were native, several other invasive species were found at low abundance at some sites during the study period: *Crangonyx pseudogracilis* (Bousfield 1958), *Potamopyrgus antipodarum* (Gray 1843) and *Dreissena polymorpha* (zebra mussel). Notably, no Ponto-Caspian shrimp of *Dikerogammarus* spp. were found in our survey. In terms of mean annual abundance, dominant native taxa across all study sites were *Gammarus pulex* (Linnaeus 1758), *Ephemera danica* (Müller 1764), *Elmis aenea* (Müller 1806) and Orthocladiinae spp. (see: **Appendix I**). Mean annual invertebrate density was consistent throughout the study reach, (range: 1300-2000 individuals m^{-2} per site) with the exception of a low figure at site 4 (c.500 ind. m^{-2}) and high at site 5 (c.2400 ind. m^{-2}). Mean annual values for

the Shannon-Weiner index of diversity were also similar throughout the study reach (range 2.0 – 2.2), but with a lower value at site 4 (1.8; **Figure 2.2**).

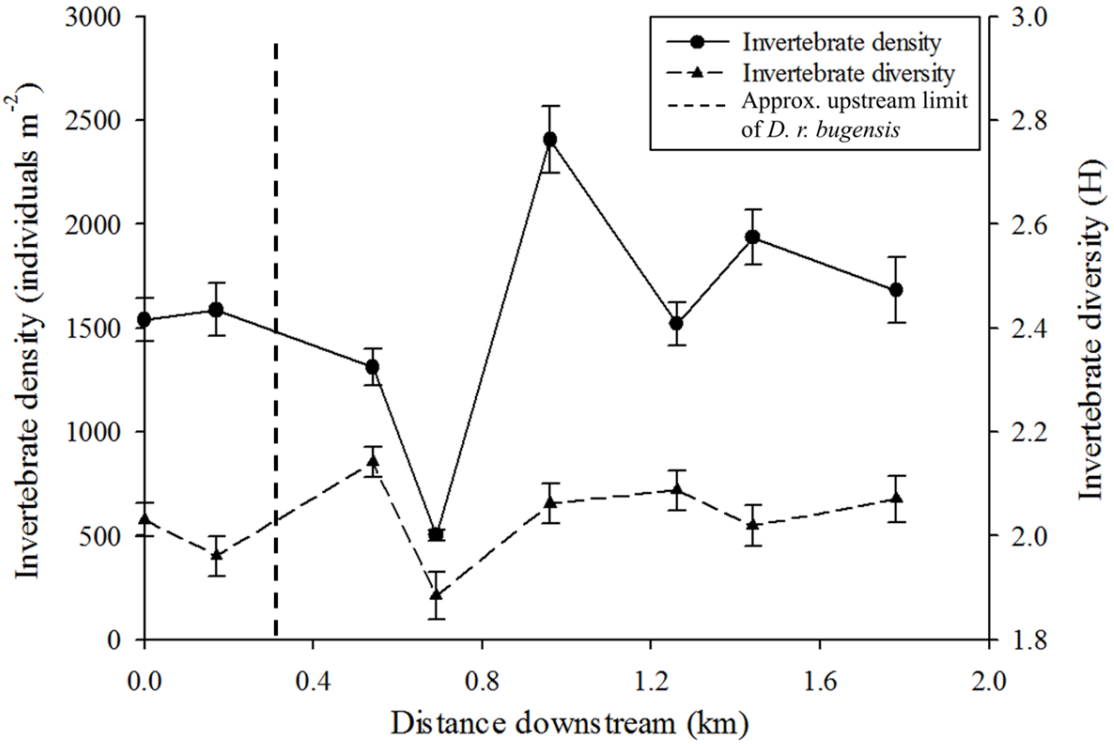


Figure 2.2 Mean annual total invertebrate density (individuals m^{-2}) and Shannon-Weiner diversity (H') scores per site with downstream distance from Site 1. Error Bars denote standard error.

Supporting physicochemical measurements presented strong homogeneity of conditions between all sites throughout the study period. Stream water pH (7.8-8.5), temperature (8-21 ^{o}C), conductivity (512-811 µs cm^{-1}), dissolved oxygen (8-14 mg L^{-1}) and flow rate (0.25-0.3 m s^{-1}) varied as expected through the year, but were very similar among study sites for each month measured (Table 2). Comparatively, measures of stream hardness (260-486 mg L^{-1} as $CaCO_3$) and alkalinity (196 -263 mg L^{-1}) varied more throughout the year; however the range of recorded mean values per site also remained small within each monthly survey (**Table 2.2**). Overall, these measurements suggested very similar physicochemical conditions across all study sites. Furthermore, values were as expected given the location, geology, seasonal climate

Table 2.2 Table of physicochemical data for stream dissolved oxygen (DO; mg L^{-1}), pH, alkalinity (mg L^{-1}), hardness (mg L^{-1} as $CaCO_3$), temperature (^oC), and flow rate (m s^{-1}). For each parameter, the range of site means, overall mean for all sites and standard error are shown per monthly sampling run.

Season and Variable	Range *site means*	Mean *all sites*	SE	Range *site means*	Mean *all sites*	SE	Range *site means*	Mean *all sites*	SE
Summer	**May 2015**			**June 2015**			**July 2015**		
Dissolved oxygen **mg L^{-1}**	10.1 - 10.3	10.2	0.06	7.4 - 8.9	8.1	0.08	8.5 - 9.2	8.9	0.04
pH	8.5 - 8.6	8.5	0.01	8.1 - 8.2	8.2	0.01	8.2 - 8.3	8.2	0.01
Conductivity **µS cm^{-1}**	792 - 810	797.5	0.02	624 - 708	652.8	5.60	526 - 576	556.3	2.60
Temp **^oC**	17.0 - 17.3	17.2	0.02	20.6 - 22	21.2	0.07	17.0 - 18.8	17.3	0.11
Hardness **mg L^{-1} (as $CaCO_3$)**	260 - 342	307.1	8.00	379 - 486	433.9	19.4	260 - 327	296.8	10.4
Alkalinity **mg L^{-1}**	196 - 286	227.8	7.72	148 - 300	195.9	12.8	224 - 277	250.1	5.00
Flow **m S^{-1}**	0.2 - 0.5	0.30	0.02	-	-	-	-	-	-
Autumn	**August 2015**			**September 2015**			**October 2015**		
Dissolved oxygen **mg L^{-1}**	7.6 - 8.2	7.8	0.02	8.3 - 8.7	8.5	0.03	8.0 - 8.5	8.2	0.03
pH	8.0 - 8.2	8.1	0.02	7.7 - 8.2	8.0	0.02	8.0 - 8.2	8.1	0.01
Conductivity **µS cm^{-1}**	426 - 584	511.5	7.60	572 - 700	613.8	7.71	640 - 658	648	7.20
Temp **^oC**	16.9 - 17.3	17.1	0.02	13.7 - 14.4	14.1	0.03	13.3 - 13.4	13.4	0.01
Hardness **mg L^{-1} (as $CaCO_3$)**	379 - 510	438.3	10.58	312 - 404	360.3	11.89	390 - 437	417.5	5.44
Alkalinity **mg L^{-1}**	203 - 234	219.8	3.81	224 - 240	231.9	1.71	197 - 211	206.4	1.50
Flow **m S^{-1}**	0.2 - 0.3	0.25	0.01	-	-	-	-	-	-
Winter	**November 2015**			**December 2015**			**January 2016**		
Dissolved oxygen **mg L^{-1}**	9.1 - 9.2	9.2	0.03	9.3 - 9.4	9.4	0.02	10.6 - 10.8	10.7	0.01
pH	7.9 - 8.0	7.9	0.01	7.8 - 7.9	7.9	0.02	7.8 - 8.0	7.8	0.02
Conductivity **µS cm^{-1}**	670 - 694	677	2.20	692 - 722	703.3	2.10	750 - 766	757.5	2.05
Temp **^oC**	11.6 - 11.7	11.6	0.01	9.7 - 9.9	9.7	0.01	8.5 - 9.1	8.9	0.03
Hardness **mg L^{-1} (as $CaCO_3$)**	281 - 381	314.6	10.11	324 - 348	337.1	7.00	326 - 376	351.1	3.92
Alkalinity **mg L^{-1}**	247 - 268	253.1	4.42	242 - 269	262.6	5.53	236 - 267	249.3	2.38
Flow **m S^{-1}**	0.2 - 0.4	0.28	0.02	-	-	-	-	-	-
Spring	**February 2016**			**March 2016**			**April 2016**		
Dissolved oxygen **mg L^{-1}**	11.4 - 11.7	11.6	0.02	13.5 - 13.8	13.7	0.02	12.0 - 12.6	12.3	0.04
pH	8.0 - 8.2	8.1	0.01	8.2 - 8.3	8.2	0.01	8.1 - 8.2	8.2	0.01
Conductivity **µS cm^{-1}**	808 - 818	811	0.01	758 - 766	760.8	1.41	756 - 766	761.5	0.84
Temp **^oC**	7.6 - 8.1	7.8	0.04	10.3 - 10.8	10.4	0.02	13.1 - 13.9	13.5	0.05
Hardness **mg L^{-1} (as $CaCO_3$)**	317 - 333	325.1	2.42	326 - 364	341.7	13.59	347 - 377	360.2	3.91
Alkalinity **mg L^{-1}**	221 - 268	238.5	3.88	233 - 286	225.0	4.42	231 - 253	242.5	2.49
Flow **m S^{-1}**	0.2 - 0.3	0.26	0.01	-	-	-	-	-	-

and previous monitoring records from the UK Environment Agency (EA., 2016; pers. com). Invaded and uninvaded site groups were very similar and could theoretically support similar ecological communities.

Mean annual taxa richness (excluding quagga mussel) was consistent between both invaded and uninvaded site groups with an exception at site 4, where it was found to be lower than all other sites (**Figure 2.3**). This pattern was maintained when data were split into seasonal means, but with generally higher richness found in the summer period (**Figure 2.3**). ANOVAs showed that mean taxa richness differed significantly between study sites in every month except April 2016. Tukey's tests showed differences were driven by lower richness at site 4 (**Table 2.3**).

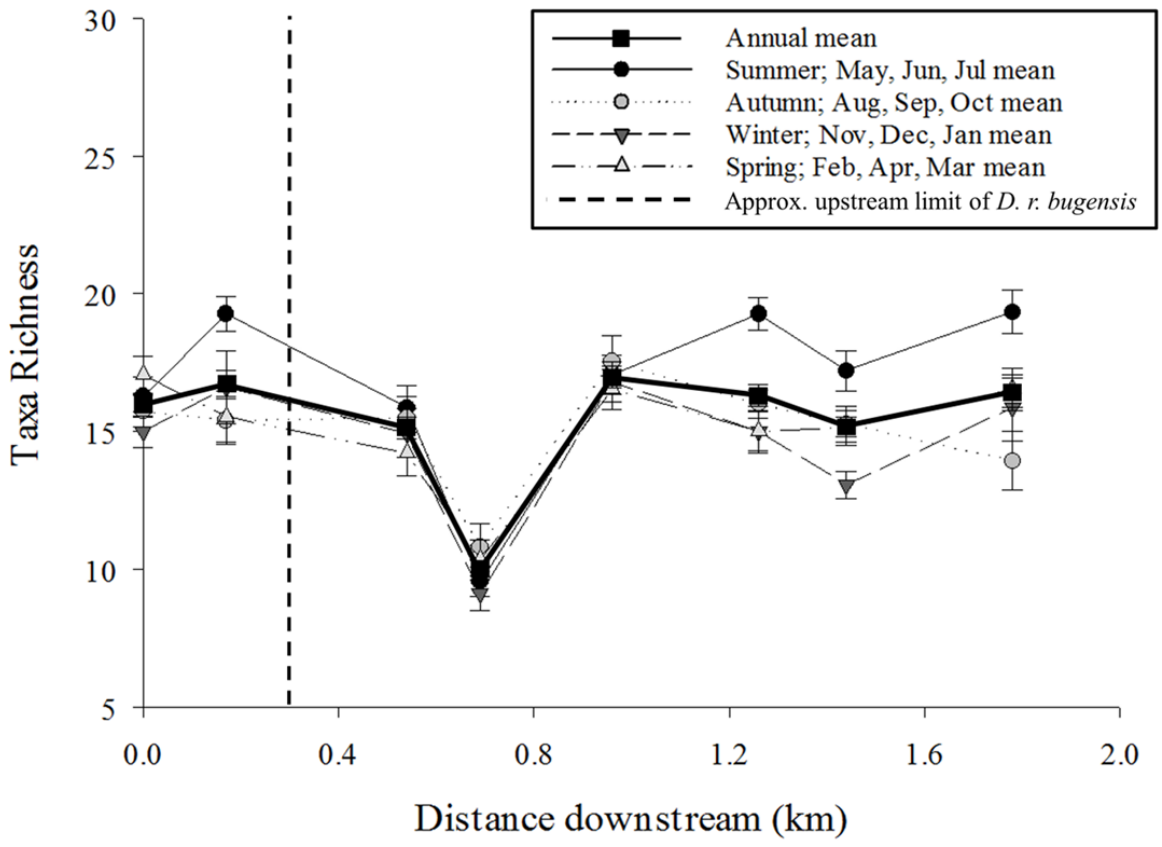


Figure 2.3 Mean annual and seasonal taxa richness with downstream distance from Site 1. Error bars denote standard error.

Mean annual biomass throughout all sites was 2.10g m^{-2} including quagga mussel and 1.00g m^{-2} excluding quagga mussel. Among invaded sites, quagga mussel contributed 61% of mean annual biomass; however this proportion was distributed with high variation throughout the study reach. While closely reflecting measured trends in quagga mussel density (**Figure 2.4b**), upstream invaded sites presented higher quagga mussel biomass in comparison to those downstream (**Figure 2.4a**). Upstream sites 3 and 4 for example, exhibited higher mean annual values of 1.61g m^2 and 4.38g m^{-2}, respectively.

Furthermore, at site 4, quagga mussel alone contributed 90% of mean annual biomass composition. In contrast, the site placed farthest downstream (site 8) gave the lowest measures of quagga mussel biomass (annual mean: 0.15 g m^{-2}), where it contributed to only 15% of mean annual biomass composition. When the data were split into seasonal means, similar trends were maintained, with both quagga mussel biomass and density higher in the winter and summer period while lower in Autumn (**Figure 2.4a & b**). ANOVAs showed that mean quagga mussel biomass differed significantly between invaded study sites for over half of the monthly measurements (**Table 2.4**). Tukey's tests showed this was primarily driven by high quagga mussel biomass at sites 3 and 4 with lower values at site 8 (**Table 2.4**).

When excluding quagga mussel, mean annual biomass of invertebrates varied less throughout the study reach and closely reflected trends in invertebrate density (**Figure 2.5a & b**). Site 4 differed for both parameters, consistently presenting lower values in comparison to other sites. Similar trends of invertebrate biomass and density (excl. quagga mussel) were maintained for seasonal means but with higher values for both evident in the summer period; particularly at the most downstream sites (**Figure 2.5a & b**).

Table 2.3 Mean monthly taxa richeness (± SE) per site (excluding *D. r. bugensis*). Results from ANOVA and Tukey's tests are also presented with significant values in bold.

Month	Site number / taxa richness								ANOVA		Tukey test
	1	2	3	4	5	6	7	8	Test	*p*- value	
May 15	16.2 ± 1.3	19.4 ± 1.4	15.4 ± 2.1	**9.2 ± 1.2**	17.2 ± 1.5	21.0 ± 0.9	19.6 ± 1.0	20.0 ± 1.2	$F_{(7, 32)} = 7.7$	<0.001***	4 < 2, 6, 7, 8
Jun 15	17.0 ± 1.5	19.6 ± 1.3	16.0 ± 0.7	**10.4 ± 1.1**	16.8 ± 1.4	18.8 ± 1.0	17.0 ± 0.8	18.8 ± 1.7	$F_{(7, 32)} = 5.4$	<0.001***	4 < 1, 4, 6, 8
Jul 15	15.6 ± 1.2	18.8 ± 0.7	16.2 ± 1.1	**9.0 ± 0.5**	17.2 ± 1.0	18.0 ± 0.7	15.0 ± 1.2	19.2 ± 1.4	$F_{(7, 32)} = 10.2$	<0.001***	4 < 2, 5, 6, 8
Aug 15	13.8 ± 0.7	14.4 ± 2.0	15.0 ± 0.9	13.0 ± 2.1	19.2 ± 1.6	16.0 ± 0.7	16.0 ± 1.4	**10.0 ± 0.9**	$F_{(7, 31)} = 3.6$	0.006**	8 < 5
Sep 15	16.8 ± 0.8	14.0 ± 0.5	15.6 ± 1.7	**9.8 ± 0.7**	18.4 ± 1.6	15.6 ± 1.1	15.2 ± 1.0	15.6 ± 1.9	$F_{(7, 32)} = 4.0$	0.003**	4 < 2, 4, 5, 6
Oct 15	16.6 ± 1.0	17.8 ± 1.3	15.8 ± 1.4	**9.6 ± 1.1**	15.0 ± 1.4	16.5 ± 1.0	14.6 ± 1.0	16.2 ± 1.4	$F_{(7, 32)} = 4.0$	0.003**	4 < 2, 8
Nov 15	14.5 ± 1.0	19.4 ± 3.0	15.8 ± 2.7	**7.2 ± 0.8**	15.0 ± 1.5	14.2 ± 2.0	12.8 ± 0.5	18.6 ± 2.5	$F_{(7, 32)} = 3.6$	0.006**	4 < 2, 8
(Ln) Dec 15	15.0 ± 1.2	14.8 ± 2.4	15.2 ± 0.7	**9.6 ± 1.1**	17.2 ± 1.1	16.2 ± 1.1	13.4 ± 0.7	14.2 ± 0.6	$F_{(7, 32)} = 3.3$	0.010*	4 < 5, 6, 3
Jan 16	15.4 ± 0.8	15.6 ± 0.7	13.8 ± 0.4	**10.6 ± 0.9**	18.2 ± 1.0	14.6 ± 0.7	13.0 ± 1.3	14.8 ± 2.4	$F_{(7, 32)} = 3.2$	0.012*	4 < 5, 2
Feb 16	17.0 ± 1.4	18.0 ± 1.2	12.6 ± 2.0	**8.8 ± 1.0**	16.8 ± 2.0	13.2 ± 0.8	14.2 ± 1.4	16.2 ± 1.5	$F_{(7, 32)} = 4.3$	0.002**	4 < 1, 2, 5, 8
Mar 16	16.6 ± 0.7	15.2 ± 1.8	16.0 ± 0.7	**10.4 ± 1.4**	17.4 ± 0.9	16.8 ± 0.9	16.6 ± 0.9	17.8 ± 1.2	$F_{(7, 32)} = 4.4$	0.002**	4 < 1, 5, 6, 8
Apr 16	17.6 ± 1.4	13.4 ± 1.2	14.0 ± 0.8	**11.8 ± 1.2**	15.4 ± 0.7	15.0 ± 1.5	14.6 ± 0.9	15.6 ± 1.3	$F_{(7, 32)} = 2.2$	0.066	-

* P < 0.05; ** P < 0.01; *** P < 0.001; ***(Ln)*** *denotes where monthly data was transformed to better meet ANOVA assumptions.*

Table 2.4 Mean monthly *D. r. bugensis* biomass (DM g m^{-2} ± SE) per site. Results from ANOVA and Tukey's tests are also presented with significant values in bold.

Month	Site number / mean biomass (DM g m^{-2})								ANOVA on Ranks		Tukey test
	1	2	3	4	5	6	7	8	Test	*p*- value	
May 15	-	-	**1.45 ± 0.3**	**6.44 ± 2.6**	0.22 ± 0.1	1.42 ± 1.0	0.61 ± 0.1	0.14 ± 0.1	$H = 14.3_{(5)}$,	0.014*	4 > 3, 8
Jun 15	-	-	**3.16 ± 1.1**	**4.54 ± 1.7**	0.32 ± 0.2	1.02 ± 0.3	0.54 ± 0.1	0.07± 0.01	$H = 19.5_{(5)}$	0.002**	4 > 8, 5 & 3 > 8
Jul 15	-	-	**2.60 ± 0.8**	2.42 ± 1.4	0.49 ± 0.2	0.32 ± 0.1	1.42 ± 0.8	0.05 ± 0.01	$H = 14.9_{(5)}$	0.011*	3 > 8
Aug 15	-	-	1.13 ± 0.6	1.73 ± 0.8	0.10 ± 0.1	0.33 ± 0.1	1.24 ± 0.5	0.18 ± 0.1	$H = 13.5_{(5)}$	0.019*	n.s
Sep 15	-	-	1.42 ± 0.8	2.04 ± 0.9	0.49 ± 0.3	0.72 ± 0.3	0.66 ± 0.3	0.22 ± 0.1	$H = 5.7_{(5)}$	0.332	-
Oct 15	-	-	1.30 ± 0.7	**2.61 ± 1.0**	0.08 ± 0.01	0.39 ± 0.2	0.79 ± 0.1	0.20 ± 0.1	$H = 14.0_{(5)}$	0.016*	4 > 5
Nov 15	-	-	0.59 ± 0.4	10.29 ± 4.3	1.47 ± 0.9	1.96 ± 1.06	1.71 ± 0.88	0.31 ± 0.2	$H = 9.0_{(5)}$	0.110	-
Dec 15	-	-	**2.30 ± 0.6**	**3.31 ± 1.7**	0.57 ± 0.3	0.56 ± 0.3	1.06 ± 0.4	0.00 ± 0.0	$H = 16.1_{(5)}$	0.007**	4 > 8 & 3 > 8
Jan 16	-	-	0.96 ± 0.4	4.79 ± 3.2	2.89 ± 1.7	0.88 ± 0.3	1.01 ± 0.4	0.01± 0.01	$H = 8.1_{(5)}$	0.150	-
Feb 16	-	-	1.47 ± 0.5	2.53 ± 0.9	2.91 ± 1.7	1.31 ± 0.5	1.33 ± 0.9	0.32 ± 0.2	$H = 7.6_{(5)}$	0.178	-
Mar 16	-	-	1.80 ± 0.7	**6.74 ± 0.3**	0.33 ± 0.04	1.65 ± 1.2	0.48 ± 0.3	0.17 ± 0.1	$H = 12.4_{(5)}$	0.030*	4 > 8
Apr 16	-	-	1.01 ± 0.4	**3.92 ± 1.7**	1.13 ± 0.7	0.59 ± 0.3	0.24 ± 0.1	0.05 ± 0.04	$H = 12.4_{(5)}$	0.029*	4 > 8

* P < 0.05; ** P < 0.01; *** P < 0.001

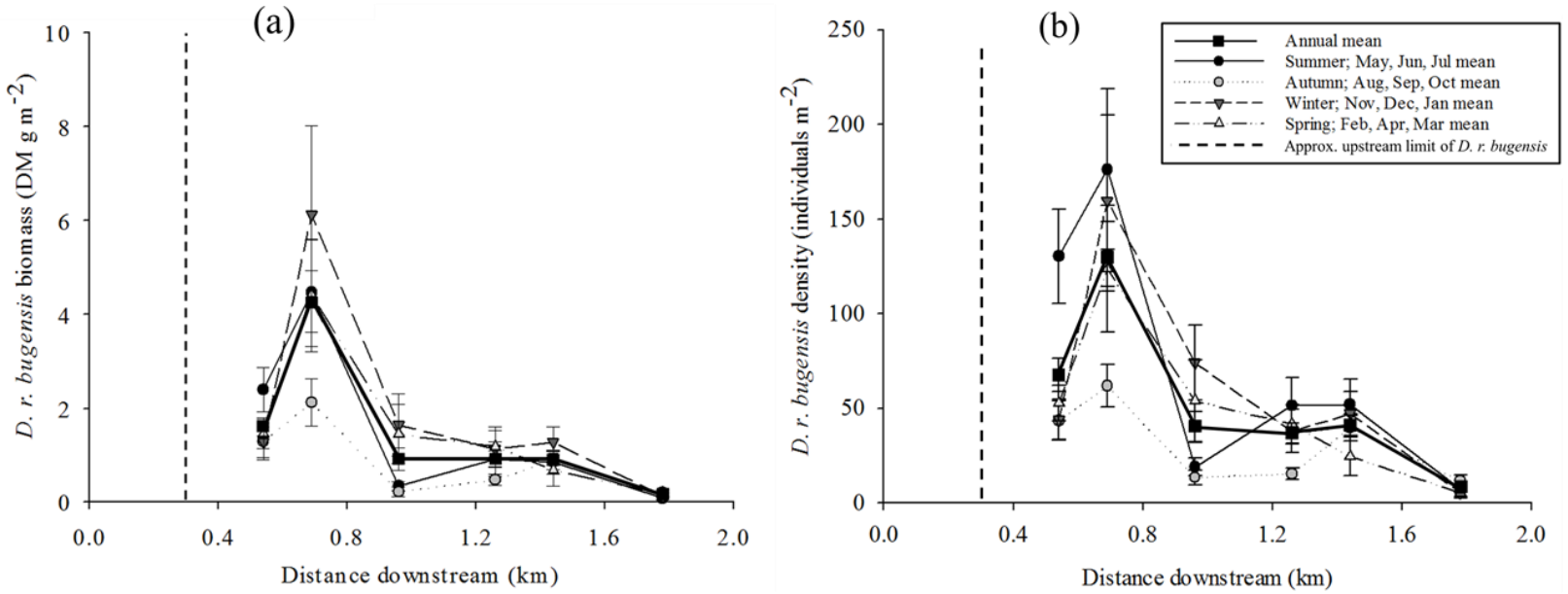


Figure 2.4 Graphs showing mean annual and seasonal (a) *D. r. bugensis* biomass (DM g m^{-2}) and (b) *D. r bugensis* density (individuals m^{-2}), with downstream distance from Site 1. Error bars denote Standard error.

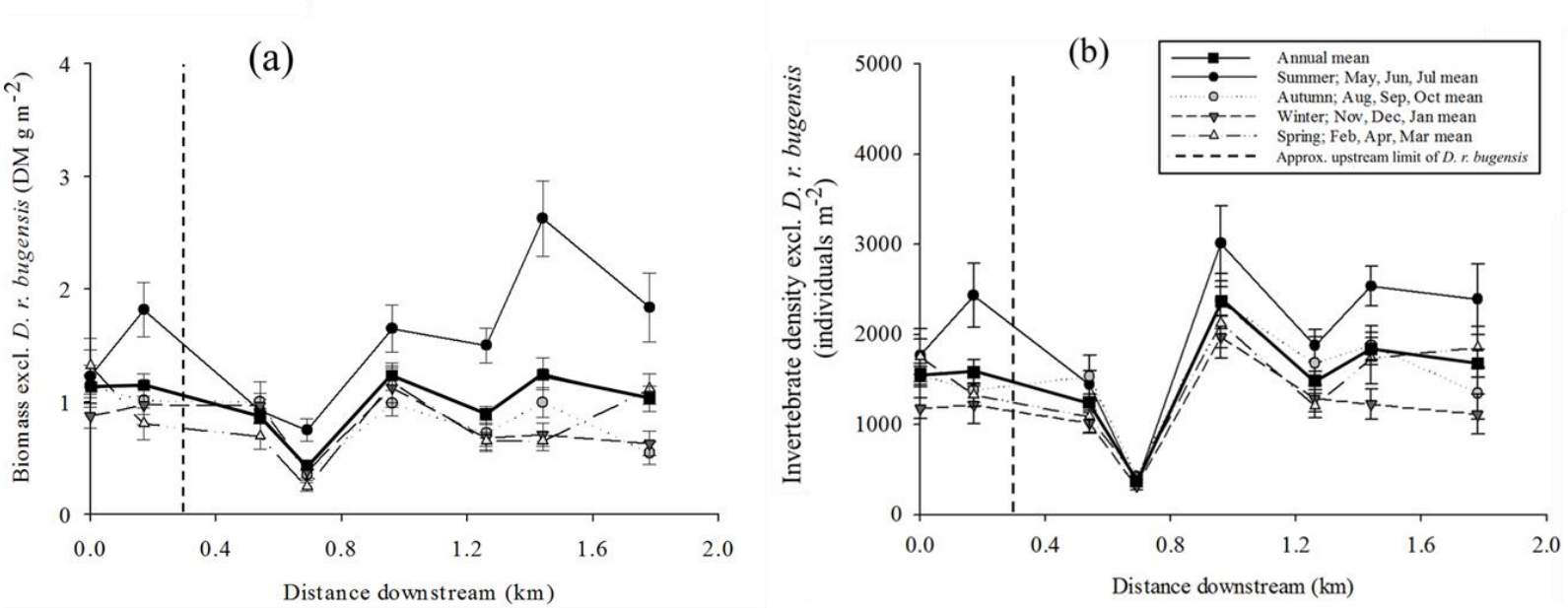


Figure 2.5 Graphs showing mean annual and seasonal (a) biomass of all taxa (excluding *D. r bugensis*; DM g m^{-2}) and (b) density of all taxa (excluding *D. r. bugensis*; individuals m^{-2}), with downstream distance from Site 1. Error Bars denote standard error.

ANOVAs on ranks presented significant differences between sites for mean invertebrate biomass in at least half the monthly measurements (**Table 2.5**), while for invertebrate density, ANOVAS showed differences in all monthly measurements (**Table 2.6**). Tukey's tests showed that in both cases this was largely driven by lower values at site 4 and in addition for density, higher values at site 5.

Analysis of mean annual invertebrate biomass by constituent feeding groups suggested that community structure at all sites was dominated by collector-gatherer taxa when excluding quagga mussel. With this analysis, collector-gatherers contributed between 60-80% of mean annual biomass at all sites (**Figure 2.6a**). In comparison, scrapers and predators consistently contributed only 0-10% throughout sites, while collector-filterers and shredders appeared to increase in importance with distance downstream. Collector-filterers (excluding quagga mussel) and scrapers rose from a 10-15% contribution to biomass at upstream sites (1-4) to between 15-25% at downstream sites (5-8).

When including quagga mussel, the contribution of collector-filterers to mean annual biomass increased significantly in invaded sites, replacing collector-gatherers as the dominant feeding group in all cases except the most downstream site (**Figure 2.6b**). This was particularly acute at the site of highest quagga mussel density (Site 4), where the contribution of collector-filterers to biomass increased from 1% to 92%. In contrast, site 8 held the lowest quagga mussel density and community structure here remained dominated by collector-gatherers. This most downstream site resembled proportional feeding group structures at the upstream, uninvaded sites (1-2).

According to the ANOSIM, moderate differences in community structure were detected between invaded and uninvaded sites based on their biomass composition throughout all

Table 2.5: Mean monthly biomass (DM g m^{-2} ± SE) per site of all taxa when excluding *D. r. bugensis*. Results from ANOVA and Tukey's tests are also presented.

Month	Site number / mean biomass (DM g m^{-2})								ANOVA		Tukey test
	1	2	3	4	5	6	7	8	Test	*p*- value	
May 15	1.70 ± 0.3	1.80 ± 0.2	0.97 ± 0.3	**0.65 ± 0.2**	1.30 ± 0.4	1.73 ± 0.2	**3.95 ± 0.4**	2.57 ± 0.6	$F_{(7, 32)}$ = 8.1	<0.001***	4 < 7, 8, & all < 7
(Ln) ***Jun 15***	1.45 ± 0.5	2.08 ± 0.4	0.96 ± 0.1	0.91 ± 0.9	1.98 ± 0.5	1.83 ± 0.3	2.45 ± 0.4	1.89 ± 0.5	$F_{(7, 32)}$ = 2.5	0.035*	n.s
(Ln) ***Jul 15***	**0.53 ± 0.1**	1.57 ± 0.6	0.84 ± 0.1	**0.69 ± 0.2**	**1.67 ± 0.2**	0.95 ± 0.1	1.48 ± 0.3	1.05 ± 0.1	$F_{(7, 32)}$ = 3.6	0.006**	1, 4 < 5
Aug 15	0.57 ± 0.1	0.81 ± 0.2	1.52 ± 0.4	**0.38 ± 0.1**	1.13 ± 0.3	0.60 ± 0.1	1.06 ± 0.3	**0.25 ± 0.1**	$F_{(7, 32)}$ = 3.5	0.007**	4 < 8, 2
Sep 15	1.00 ± 0.2	0.88 ± 0.2	0.59 ± 0.2	0.31 ± 0.1	0.9 ± 0.1	0.83 ± 0.2	1.08 ± 0.3	0.68 ± 0.2	$F_{(7, 32)}$ = 1.7	0.152	-
Oct 15	**1.85 ± 0.3**	1.33 ± 0.2	1.00 ± 0.2	**0.38 ± 0.1**	0.94 ± 0.1	0.74 ± 0.3	0.85 ± 0.2	0.71 ± 0.2	$F_{(7, 32)}$ = 4.9	<0.001***	4, 6, 7, 8 < 1 & 4 < 2
Nov 15	0.50 ± 0.1	1.12 ± 0.4	1.07 ± 0.3	0.33 ± 0.1	0.66 ± 0.2	0.48 ± 0.2	0.67 ± 0.2	0.58 ± 0.1	$F_{(7, 32)}$ = 1.6	0.173	-
(Ln) ***Dec 15***	1.21 ± 0.1	1.03 ± 0.4	1.12 ± 0.2	**0.40 ± 0.1**	1.25 ± 0.2	0.84 ± 0.2	0.74 ± 0.1	0.60 ± 0.1	$F_{(7, 32)}$ = 3.4	0.007**	4 < 1, 3, 5
(Ln) ***Jan 16***	0.92 ± 0.1	0.76 ± 0.1	0.71 ± 0.6	0.44 ± 0.1	1.46 ± 0.4	0.71 ± 0.3	0.72 ± 0.2	0.71 ± 0.3	$F_{(7, 32)}$ = 1.7	0.154	-
(Ln) ***Feb 16***	1.36 ± 0.6	1.15 ± 0.3	0.70 ± 0.3	**0.20 ± 0.3**	1.01 ± 0.5	0.66 ± 0.2	0.52 ± 0.1	1.02 ± 0.3	$F_{(7, 32)}$ = 2.5	0.035*	4 < 1, 2
Mar 16	0.71 ± 0.2	0.66 ± 0.2	0.68 ± 0.1	**0.15 ± 0.1**	1.12 ± 0.2	0.61 ± 0.1	0.45 ± 0.1	**1.22 ± 0.1**	$F_{(7, 32)}$ = 5.5	<0.001***	4 < 8, 5 & 7 < 8
Apr 16	**1.89 ± 0.3**	0.60 ± 0.1	0.70 ± 0.2	**0.39 ± 0.1**	1.28 ± 0.2	0.68 ± 0.1	0.98 ± 0.2	1.11 ± 0.3	$F_{(7, 32)}$ = 6.5	<0.001***	4 < 1, 5, 8, 7 & 2, 3, <1

* P < 0.05; ** P < 0.01; *** P < 0.001; ***(Ln)*** *denotes where monthly data was transformed to better meet ANOVA assumptions.*

Table 2.6 Mean monthly invertebrate density (individuals m^{-2} ± SE) per site when excluding *D. r. bugensis*. Results from ANOVA and Tukey's tests are also presented.

Month	Site number / mean invertebrate density (individuals m^{-2})								ANOVA		Tukey test
	1	2	3	4	5	6	7	8	Test	*p*- value	
(Ln) ***May 15***	2159±485	1764±334	1537±415	**274±78**	2879±743	2132±405	3022±171	3364±999	$F_{(7, 32)}$ =10.5	<0.001***	4< 5, 6, 7, 8
(Ln) ***Jun 15***	2236±594	3373±873	1453±124	**312±67**	4054±878	2088±286	3046±299	3046±494	$F_{(7, 32)}$ =13.0	<0.001***	4< 2, 5, 6, 7
(Ln) ***Jul 15***	905±153	2161±324	1344±195	**453±28**	**2100±156**	1405±110	1533±104	1797±141	$F_{(7, 32)}$ =20.9	<0.001***	4< 1, 2, 3, 5, 7 & 5 > 1
Aug 15	1186±222	1520±368	1432±368	**510±91**	**2752±538**	1416±302	**2324±410**	391±116	$F_{(7, 32)}$ = 5.4	<0.001***	4< 5, 7, & 5 > 8 & 7 > 8
(Ln) ***Sep 15***	1581±155	1509±125	1318±430	**384±71**	2824±554	2218±746	1643±317	1327±157	$F_{(7, 32)}$ = 7.4	<0.001***	4< 1, 5, 6, 7
Oct 15	1873±214	1113±148	1539±451	**384±85**	1523±336	1070±526	837±374	1665±619	$F_{(7, 32)}$ = 2.7	0.026*	4< 1, 8
(Ln) ***Nov 15***	736±188	1263±355	1162±327	**202±29**	1509±491	1135±240	1637±360	1752±530	$F_{(7, 32)}$ = 6.0	<0.001***	4< 1, 5, 6, 7
(Ln) ***Dec 15***	1146±276	1408±539	1091±107	**296±39**	**2392±366**	1774±161	942±131	610±63	$F_{(7, 32)}$ =13.5	<0.001***	4< 1, 2, 5, 6, 7, & 5 > 4
Jan 16	1114±108	975±84	793±49	**453±93**	**2005±322**	951±238	1087±287	975±232	$F_{(7, 32)}$ = 4.8	<0.001***	4< 1, 5 & 5 > 2, 3, 6, 8
Feb 16	1592±186	1390±166	722±85	**255±47**	1272±300	955±265	1065±204	1660±405	$F_{(7, 32)}$ = 4.0	0.003**	4< 1, 2, 8
Mar 16	1113±99	960±110	1030±156	**404±55**	**1722±279**	1190±94	1228±153	1562±101	$F_{(7, 32)}$ = 7.5	<0.001***	4< 5, 6, 7, 8, & 5 > 2, 3
Apr 16	2543±314	1621±272	1509±456	**553±75**	**3371±112**	1480±275	2908±506	2337±545	$F_{(7, 32)}$ = 6.5	<0.001***	4< 1, 5, 7, 8 & 5 >, 3, 6

* P < 0.05; ** P < 0.01; *** P < 0.001; ***(Ln)*** *denotes where monthly data was transformed to better meet ANOVA assumptions.*

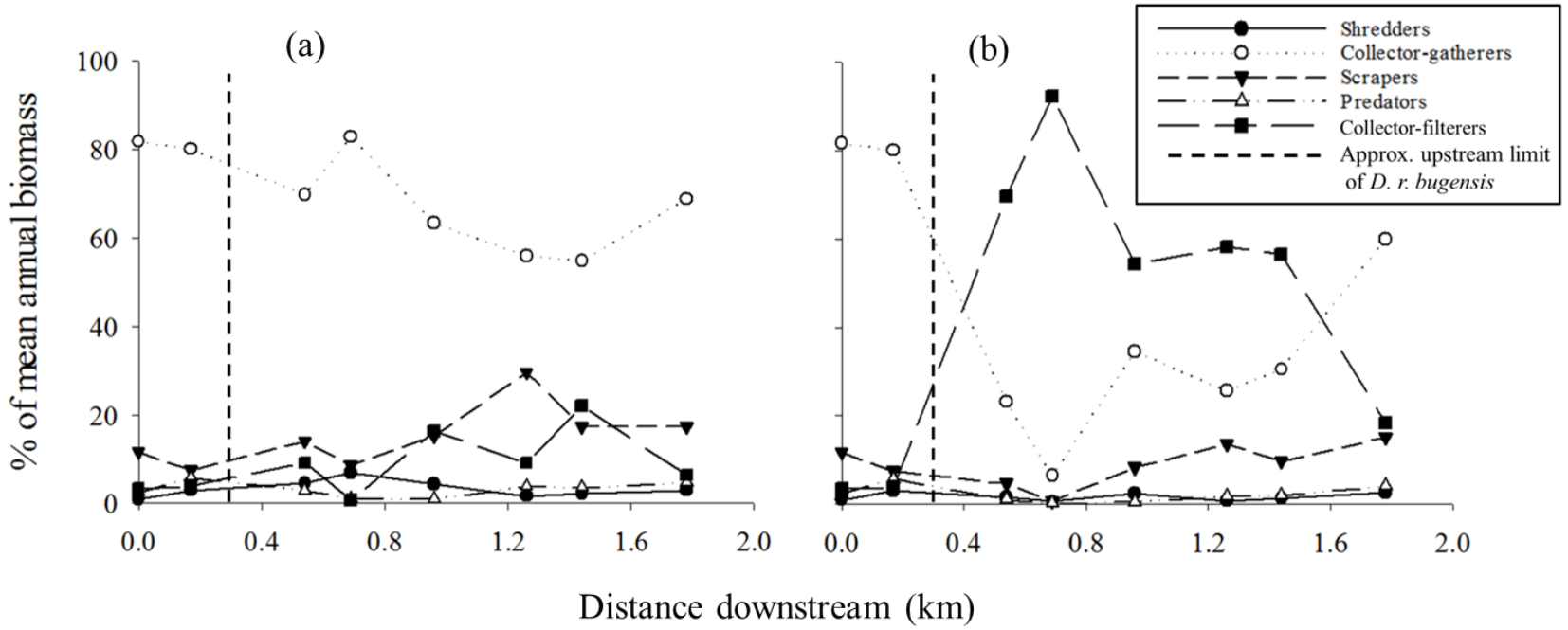


Figure 2.6 Percentage of mean annual biomass apportioned to functional feeding groups present with downstream distance from site 1 (a) excluding *D. r. bugensis* and (b) including *D. r. bugensis* (as collector-filterers).

monthly data sets (R = 0.417). A segregation of site groups was detected with the NMDS using the mean annual plot coordinates for each site (**Figure 2.7**). Moderately invaded sites (3, 5-7) were strongly grouped near site 8, where the lowest quagga mussel density was found. The heavily invaded site 4 and uninvaded sites (1-2) each occupied distinct spaces on opposite sides of the plot with the site farthest downstream (8) placed closest to the uninvaded sites (1-2). The positioning of invertebrate taxa, including *D. r. bugensis*, was less clearly patterned. The majority of taxa clustered near the centre of the ordination plot with rarely occurring taxa (e.g. *R. peregra* (Müller, 1774) and *E. octoculata* (Linnaeus, 1758)) placed as relative outliers. The latter is an expected artefact of the technique (Clarke and Green 1988).

The SIMPER analysis showed 33% dissimilarity in mean biomass composition between uninvaded and invaded site groups, based on a mean of all monthly data sets (**Table 2.7**). Quagga mussel biomass contributed the most to this value (29% dissimilarity) with the caseless caddis *Hydropsyche* spp. (Curtis 1834) and mollusc *Theodoxus fluviatalis* (Linnaeus 1758) also prominent (both driving 7% dissimilarity).

Table 2.7. Results of a SIMPER analysis to determine the contribution of important taxa to mean dissimilarity of biomass (DM g m^{-2}) between uninvaded and invaded sites, based on all months (top 12 taxa only).

Test Groups	Mean Dissimilarity (%)	Species	Dissimilarity (%)	Cumulative Dissimilarity (%)
Uninvaded v Invaded Sites (1-8)	**33.23**	***D. r. bugensis***	28.6	28.60
		Hydropsyche spp.	7.18	35.78
		T. fluviatalis	6.52	42.3
		B. rhodani	6.09	48.39
		L. volkmarki	6.05	54.44
		Limnephilidae spp.	5.79	60.23
		Simulium spp.	5.67	65.9
		G. pulex	4.70	70.6
		C. splendens	4.52	75.12
		E.aenea	4.36	79.48
		E. danica	3.68	83.16
		B. tentaculata	3.21	86.37

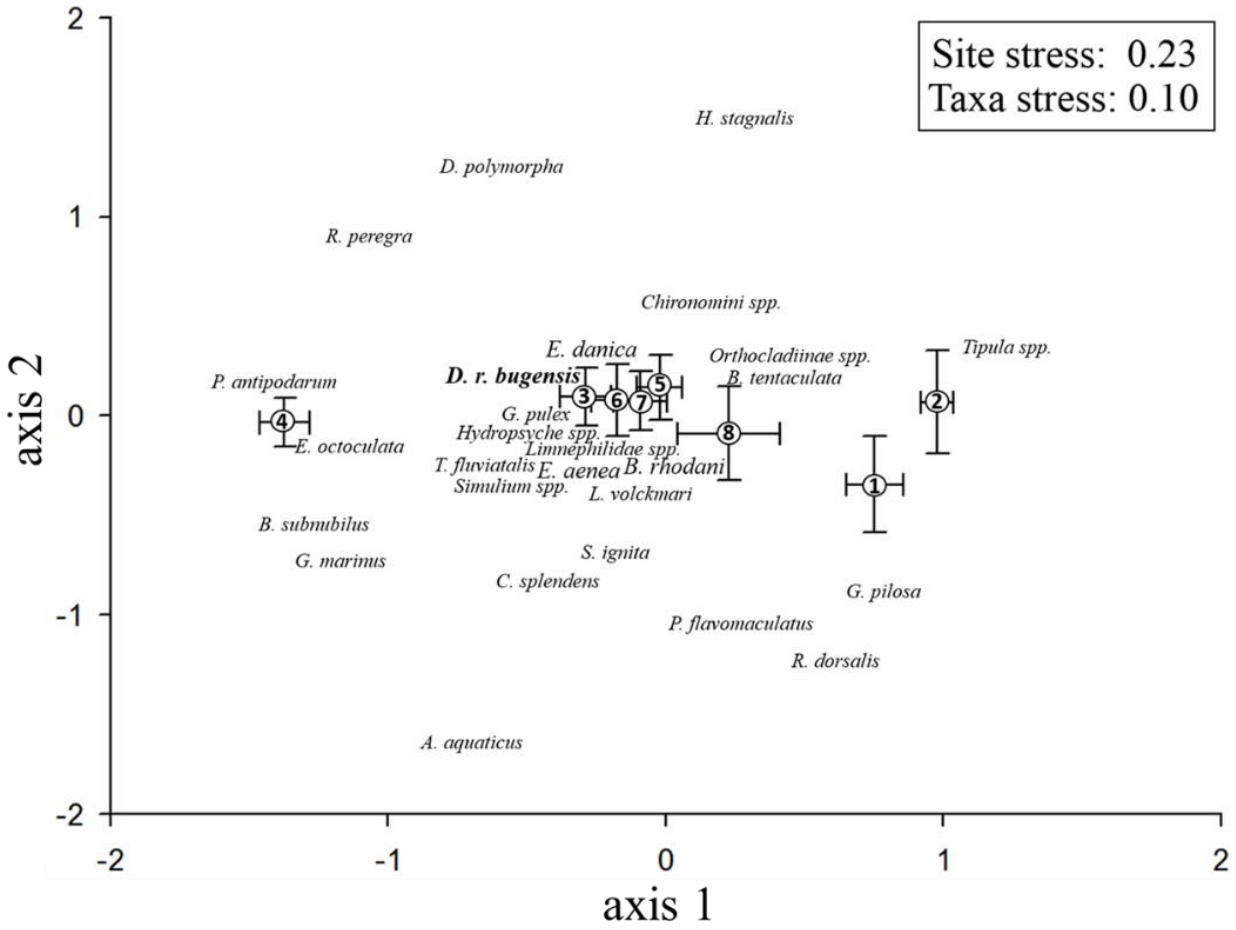


Figure 2.7 Non-metric Multidimensional Scaling (NMDS) ordinations of Bray-Curtis similarities in mean annual biomass composition both between sites (± SE) and taxa.

The SIMPER analysis also presented high within-group similarity of uninvaded and invaded sites at 76% and 75%, respectively (**Table 2.8**). For both categories, the same five native taxa contributed most to within group similarity when excluding quagga mussel. These were *Gammarus pulex*, (24% uninvaded sites; 16% invaded sites), *Ephemera danica*, (22% uninvaded sites; 15% invaded sites), *Elmis aenea*, (10% uninvaded sites; 6% invaded sites), *Limnius volckmari*, Panzer 1793 (10% uninvaded sites; 10% invaded sites), and *Hydropsyche* spp. (7% uninvaded sites; 7% invaded sites). Quagga mussel also contributed strongly towards defining the invaded site group (19%).

Table 2.8 Results of a SIMPER analysis to determine the contribution of important species to mean similarity of biomass (DM g m^{-2}) within uninvaded and invaded site groups, based on all months (*D. r. bugensis* and top 5 other taxa only).

Test Group	Mean Similarity (%)	Species	Similarity (%)	Cumulative Similarity (%)
Uninvaded Sites (1-2)	**76.46**	*G. pulex*	24.15	24.15
		E.danica	21.81	45.97
		E.aenea	10.09	56.06
		L. volckmari	10.05	66.11
		Hydropsyche spp.	6.78	72.89
Invaded Sites (3-8)	**75.80**	***D. r. bugensis***	19.12	19.12
		G. pulex	15.83	34.95
		E. danica	15.46	50.41
		L. volkmarki	9.69	60.10
		Hydropsyche spp.	6.75	66.85
		E. aenea	6.27	73.12

Discussion

Quagga mussel was consistently found in the Wraysbury River downstream of the reservoir pump facility situated between invaded and uninvaded site groups. The highest estimate of mean annual biomass for the species at any one site (4.4 g m^{-2}; site 4) was markedly lower than comparable mean figures from the Great Lakes Michigan (28.6g m^{-2}; Nalepa et al. 2009), Erie (24.7g m^{-2}; Patterson et al. 2005), and Ontario (86.9g m^{-2} ;Wilson et al. 2006). Within invaded reaches the proportion of invertebrate biomass associated only with quagga mussel (annual mean: 61%) was lower than comparable values reported for sites at Great Lakes Erie (91%; Dermott and Kerec 1997), Ontario (98%; Birkett et al. 2015) and a series of smaller waterbodies within Eastern Europe (all >93%; Burlakova et al. 2005). It is possible that our lower results reflect natural differences in the habitability of lotic and lentic systems for quagga mussel. For example, increased variation in planktonic food availability (Lucy et al. 1998),

veliger larvae survival (Stoeckel et al. 1997) and ultra-violet light exposure at shallow stream depths (Aldridge 2014) may limit *Dreissena* spp. success in riverine systems.

When excluding quagga mussel, mean invertebrate richness, biomass and density were significantly different between sites for at least half of monthly measurements; though patterns were largely driven by lower values at only one site (4). With similar indications apparent for Shannon-Weiner diversity (H'), such results were unexpected because relatively widespread impacts of *Dreissena* spp. invasions on benthic community structure have been reported from other studies (e.g. Stewart and Haynes 1994; Karatayev 1997; Ricciardi et al. 1997; Karatayev et al. 2002; Higgins and Vander Zanden 2010). Records from the Great Lakes region in particular show marked increases in taxa richness and biomass in response to *Dreissena* spp. colonisation (Burlakova et al. 2012; Karatayev et al. 2015). In such cases *Driessena* spp. beds may facilitate other taxa by physically enhancing habitat heterogeneity and providing an additional food source with their pseudofaeces (Botts et al., 1996; Burlakova et al. 2012). Significantly, our results did not provide convincing evidence for comparable processes in the Wraysbury River. This was despite a clear segregation of uninvaded and invaded sites shown in the NMDS plot (Figure 2.7).

Expected differences in the biomass and density of certain taxa groups were not found. Prominent resident natives such as *Gammarus pulex* maintained consistent biomass and density throughout the study reach, with the exception of lower values at the site of highest quagga mussel density (Site 4; Appendix I). This was in contrast to comparable taxa previously being shown to respond positively to *Dreissena* spp. colonisation (e.g. Stewart and Haynes 1994; Ricciardi et al. 1997; Dermott et al. 1998; Stewart et al. 1998). Additionally, other collector-filterers were thought to be among the most vulnerable to *Dreissena* spp. invasions due to direct trophic competition (Karatayev et al. 1997 Strayer et al. 1999). Despite this, the major collector-filterer present (caseless caddis *Hydropsyche* spp.) was found at higher densities

within invaded sites (Appendix I). Indeed, when excluding quagga mussel, the proportion of mean annual biomass represented by collector-filterers increased downstream (Figure 2.6a). While such trends are consistent with predictions of the River Continuum Concept (Vannote et al. 1980), the homogenous and localised nature of the study reach would likely preclude such effects normally found at a much larger catchment-scale.

The 'within group' SIMPER analysis also provided limited evidence for expected differences between uninvaded and invaded sites. With the exclusion of quagga mussel the same five taxa contributed most towards the mean biomass composition of both invaded and uninvaded site groups when incorporating all monthly data sets (Table 2.8; *Gammarus pulex*, *Ephemera danica*, *Elmis aenea, Limnius volckmari* and collector-filterer *Hydrophsyche* spp.). Again this contrasts with the lentic literature, where shifts in dominant faunal groups have been observed after colonisation (e.g. Stewart and Haynes 1994; Burlakova 2005; Nalepa et al. 2009). It is possible that compared to the large, deep, lentic systems of these studies, the low quagga mussel densities recorded in Wraysbury River are insufficient to produce comparable faunal shifts. In particular, the complex mussel beds expected to provide habitat space and refugia for other invertebrate species (Stewart et al. 1998; Bailly and MacIsaac 2000; Ricciardi 2001; Burlakova et al. 2012) are likely to be absent or comparatively underdeveloped at lower densities.

The relatively homogenous assemblage of native invertebrates between invaded and uninvaded sites suggests that for the Wraysbury River, the clustering of sites presented in the NMDS plot (Figure 2.7) was driven by the biomass of quagga mussel alone. This is strongly supported by the 'between group' SIMPER analysis (Table 2.7) which presented quagga mussel as a large contributor (~29%) towards mean dissimilarity among site groups. However, it is important to reassert that at site 4, where the highest quagga mussel biomass and density was found, there was a significant reduction in mean invertebrate richness, biomass and density for over half the

monthly measurements when excluding quagga mussel. While again contrary to expectations of general community facilitation derived from the lentic literature, it suggests that such densities of quagga mussel (site 4 annual mean: 130 individuals m^{-2}) can cause loss of taxa in river ecosystems. Considering the fauna of the Wraysbury River, it is possible that such densities of mussel may form a barrier to surficial bed substrate preferred by locally dominant taxa such as the burrowing mayfly *Ephemera danica* and riffle beetles of family Elmidae. In time, these taxa could be replaced with a shift to different faunal groups at site 4, better reflecting trends described in lentic literature. Further monitoring would be required to observe possible shifts in invertebrate community structure, and caution should be taken to ensure that no unconsidered physicochemical differences confound findings between sites.

This study represents a first benchmark for understanding the progression and impacts of quagga mussel invasions in UK Rivers. Additional research might address why quagga mussel biomass found at the upstream invaded sites (3 & 4) was relatively high. This may be due to unconsidered factors of habitat suitability or the average settling distance of quagga mussel veligers from the reservoir pump facility. Indeed, the upstream proximity of well-established adult colonies to source veliger larvae is considered important for *Dreissena* spp. distribution in the North American Great Lakes region (Hovarth and Lamberti 1999; Stoeckel et at. 1997) and river Don & Volga basins of Russia (Zhulidov et al. 2005). For the Wraysbury River, a source colony could be represented by the reservoir pump between sites 2 and 3.

The comparatively low quagga mussel biomass downstream of sites 3 and 4 (Figure 2.4) may alternatively be due to self-limitation effects of the species. It has been thought that upstream colonies of *Dreisenna* spp. could limit seston availability for collector-filterers further downstream (Strayer et al. 1996: Fuentes 2003). Such a role would potentially cause quagga mussel to self-regulate their own population and that of other collector-filterers in the Wraysbury River. It should be noted however, that our results presented a strong community

of native collector-filterer taxa downstream of sites with the highest quagga mussel density. Further study might be undertaken to determine whether the dominant native collector-filterer in Wraysbury River (*Hydropsyche* spp.) may favour different sized planktonic food to that consumed by quagga mussel. Invertebrate feeding groups as described in this study are only categorised by the food acquisition method, not by the properties of food eaten (*sensu* Cummins and Klug 1979).

Conclusions

It is clear from this study that quagga mussel is well established in the Wraysbury River. Throughout an annual period of monthly sampling it was consistently found in sites downstream of a reservoir pump facility and in some cases comprised a significant proportion of total benthic biomass. In general however, quagga mussel biomass (both in amount and as a proportion of total benthic biomass) was not as high as that seen from studies in lentic systems.

Ordination analysis of mean biomass composition per site (when incorporating all monthly data sets) presented a segregation of uninvaded and invaded sites on the Wraysbury River. Despite this, the composition of fauna when excluding quagga mussel was found to be relatively homogeneous throughout. SIMPER analysis confirmed that the largest differences in community structure between invaded and uninvaded site groups was simply due to the presence of quagga mussel itself. Furthermore, changes to particular taxa in invaded sites were not identified as expected. When excluding quagga mussel, supposedly vulnerable collector-filterers were found to increase in importance within downstream invaded sites and the same five taxa contributed most to biomass composition within invaded and uninvaded site groups.

One site of high mussel density proved exceptional however, where quagga mussel formed a particularly large proportion of benthic biomass (site 4). Converse to expectations from lentic

literature; mean invertebrate richness, biomass and density (all when excluding quagga mussel) was consistently lower here than at other sites. While caution should be taken to account for unconsidered confounding factors; it is possible that if quagga mussel were to increase to similar densities throughout the entire river, more significant changes to native community structure might be expected in future.

Excluding quagga mussel, invertebrate community structure in Wraysbury River appears conserved at present. However, that this study is limited as it lacks pre-invasion data and it is also difficult to accurately ascertain the length of time since initial colonisation. The success and impact-magnitude of *Dreissena* spp. invasions are likely to vary temporally (Strayer and Malcom 2006; Karatayev et al. 2015) and there is need for regular, long term sampling of stream macroinvertebrates and other taxonomic groups to provide a clearer picture of post-establishment shifts in community structure. Using this study as a base line, progress in these areas would contribute towards knowledge of ecological impacts following *Dreissena* spp. invasions in rivers.

Chapter 3: Artificial substrate experiments to investigate potential impacts of invasive quagga mussel (*Dreissena rostriformis bugensis*, Bivalva: Dreissenidae) on macroinvertebrate communities in a UK river.

Summary:

Predicting potential impacts of a new invasive species remains difficult. A group of particular concern in the UK are freshwater invertebrates from the Ponto-Caspian region, including the recently established quagga mussel (*Dreissena rostriformis bugensis*, Bivalva: Dreissenidae). Invertebrate colonisation was assessed across a series of manipulated substrate tiles with gradated densities of *D. r. bugensis* shells fixed to their surface (2220, 1111, 666, 222 and 0 individuals m^{-2}). Across three experiments of different substrate tile deployment duration (14, 30 and 62 days), significant differences in invertebrate density and richness was observed among shell density treatments.

Variation was primarily driven by low and high values on the control and highest substrate shell treatments, respectively. Within each experiment, similar taxa appeared to benefit from the physical effects of *D. r. bugensis* shells (e.g. *Gammarus pulex*, *Chironomidae* spp. *Elmidae* spp. and *Hydropsyche* spp.) and were found with greater abundance on substrate tiles with higher *D. r. bugensis* shell treatments. Compared to invertebrate density, the response of taxonomic richness was weaker and only significant within our 30 and 62 day experiments of longer substrate tile deployment duration. Regardless, increased invertebrate density and richness across the highest shell treatments provided a strong indication of potential *D. r. bugensis* impacts on macroinvertebrates in the study river. If mussel densities were to increase to equivalent levels in UK rivers, similar impacts on benthic fauna would be expected to occur. While the likelihood of *D. r. bugensis* achieving such population densities are uncertain in such environments, these experimental results were considered conservative because they did not account for additional facilitative impacts associated with live mussels.

We add that in the context of invasive species management, potential facilitation of native benthic fauna associated with *D. r. bugensis* in the UK should not be considered positively, nor necessarily sustainable. Further, facilitative effects could assist the establishment of other invasive invertebrates such as amphipods of *Dikerogammarus* spp., which were first recorded in the study river during this investigation.

Publication note for chapter:

This study is in late stage of review as a research article for the journal *Aquatic Invasions*. The provisional title:

Mills DN, Chadwick MA, Francis RA (2019) Artificial substrate experiments to investigate potential impacts of invasive quagga mussel (Dreissena rostriformis bugensis, Bivalva: Dreissenidae) on macroinvertebrate communities in a UK river. *Aquatic Invasions* 14(2): 365-383, doi: https://doi.org/10.3391/ai.2019.14.2.13

Accordant to Kings College London rules on theses incorporating publication, the following is presented as for the manuscript in review, except for references which have been collated with others for this dissertation at the end of the document (from 213 pp.).

Introduction

Proliferation of non-native invasive species has been documented in freshwater environments throughout the world (Lodge et al. 1998; Francis and Chadwick 2012). While researchers have had some success recording impacts of invasive taxa on native biological communities (e.g. Gherardi and Acquistapace 2007; Stiers et al. 2011; Boltovskoy and Correa 2015), predicting impacts of a newly established species remains difficult (Williamson 1999; Roy et al. 2014). Impacts vary over time and across regions for different invasives (Strayer and Malcom 2006); potentially peaking only after considerable lag periods (Crooks 2005; Ricciardi et al. 2013).

Invasion biologists have modelled potential impacts of invasive taxa using expert knowledge and available literature (e.g. Copp et al. 2009; Roy et al. 2014) alongside statistical extrapolation of known trends (e.g. Ricciardi 2003; Kulhanek et al. 2011*a*). Problematically, where establishments occur in a novel region, prediction of future impact is difficult in the absence of robust baseline information (Kulhanek et al. 2011). Even local records of biophysically similar invasive taxa may ignore important species-specific traits (Ricciardi 2003). This is an issue because accurate future impact scenarios are important to authorities for determining resource allocation in management (Byers et al. 2002).

A group of invasive freshwater taxa of particular concern in the UK are invertebrates of the Ponto-Caspian region of Ukraine and Russia (Gallardo and Aldridge 2013; Gallardo and Aldridge 2015). In October 2014, a bivalve mollusc from this group, the quagga mussel (*Dreissena rostriformis bugensis*; Andrusov, 1897) was first recorded in the United Kingdom (Aldridge 2014). Prior to discovery, it was considered by experts as the most threatening potential invasive for the UK in terms of biodiversity impact (Roy et al. 2014). While subsequent study on invertebrate community structure in an invaded habitat did not suggest clear impacts to native biodiversity (Mills et al. 2017; **Chapter 2** 30 pp.); the known range and

densities of quagga mussel in the region appear to be increasing (Zoological Society of London, pers. com. 2017) and stronger impacts of *D. r. bugensis* may be expected at higher densities.

The establishment of invasive *Dreissena* spp. has been widely associated with shifts in the structure of pre-existing freshwater communities. In particular, invasions have been linked with increased benthic invertebrate density (Ricciardi 2003; Yakovleva and Yakovlev 2011; Ward and Ricciardi 2007). The structural complexity of *Dreissena* spp. mussel beds provide predator refugia (González and Downing 1999; Ward and Ricciardi 2007), protection from wave action (Ricciardi et al. 1997) and increased habitable surface area (Stewart et al. 1998) to facilitate invertebrate taxa. Further, grazing herbivorous species may benefit from biofilm development on mussel shells (Kobak et al. 2013) and *Dreissena* spp. pseudofaeces excretion can provide an exploitable food source for detritivores (Izvekova and Lvova-Katchanova 1972; Gergs and Rothhaupt 2008). While antagonistic biofouling of Unionid mussels and feeding competition with other filterers may cause deleterious impacts to certain taxa (Schloesser et al. 1998; Sousa et al. 2011), species of omnivorous Amphipoda and grazing Gastropoda have been shown to benefit significantly from invasions, alongside overall increases to invertebrate taxonomic richness (MacIsaac 1996; Ricciardi et al. 1997; Bially and MacIsaac 2000). Facilitative impacts of *Dreissena* spp. may also favour other invasive species; particularly from the Ponto-Caspian region, increasing risk of 'Invasional Meltdown' processes (Gallardo and Aldridge 2015; *sensu* Simberloff and Von Holle 1999).

Given such issues, the first objective of this study was to simulate and measure potential impacts of *D. r. bugensis* in UK rivers at densities higher than currently found. Invasive *Dreissena* spp. have shown varied population trends over time (Haynes et al 1999; Strayer and Malcom 2006). In the Great Lakes Region, for example, peak mussel densities were achieved after 10 years since first record in Lake Michigan (Fahnenstiel et al. 2010), 6 years in Lake Erie (Karatayev et al. 2014) and 1 year in Lake Huron (Nalepa et al. 2003). In the UK, the

zebra mussel (*Dreissena polymorpha*; Pallas, 1771) recently and unexpectedly increased its range and density, over a century after first national record and for uncertain reasons (Aldridge et al. 2004). If at any point, *D. r. bugensis* populations were to similarly expand in UK rivers, we might expect greater impacts than currently found. By simulating such an incidence here, we improve knowledge of this highly concerning invasive species in the absence of sufficient baseline data for UK rivers.

Using an experimental approach, we aimed to observe invertebrate colonisation across a series of manipulated substrate tiles treated with different densities of *D. r. bugensis* specimens; including some higher than currently recorded in the UK. Due to biosecurity considerations, we could not use live quagga mussels and so simulated *D. r. bugensis* individuals through the use of dead shell analogues. It was expected that substrate tiles with higher shell treatment densities would present increased invertebrate density and richness following deployment in a UK river. A second objective was to evaluate our novel methodology as a quantitative approach to determine potential impacts of invasive *D. r. bugensis* in the UK.

Methodology

Study Area

Manipulated substrate tile experiments were conducted in the Wraysbury River (Aldridge et al. 2014; Mills et al. 2017), a shallow tributary of the river Thames (< 0.5m depth), short in length (c. 8.7km) and situated near Staines-upon-Thames (western London; **Figure 3.1a**). Catchment geology is Devensian gravels and the river had a predominantly sandy gravel/pebble substrate with laminar, glide flow conditions throughout. Surrounding land uses include semi-natural moorland, disused canals, sparse suburban housing and a section of the London orbital motorway (M25). Seasonal records collected by the UK Environment Agency

between January 2015 and April 2017 gave mean nutrient concentrations for the Wraysbury River as total oxidised nitrogen 10.7 N mg L^{-1}, and orthophosphate 2.7 mg L^{-1} with stream alkalinity as 223 mg L^{-1} as CaCO3 (EA, pers. com. 2018). The reach in which we deployed our substrate tiles was 20m long (Lat 51.451842; Long -0.520814). It was chosen for homogeneous stream width (5m), depth (0.3-0.4m), flow velocity (0.2-0.3m s^{-1}) and substrate typology, which was sandy pebble-gravel dominated.

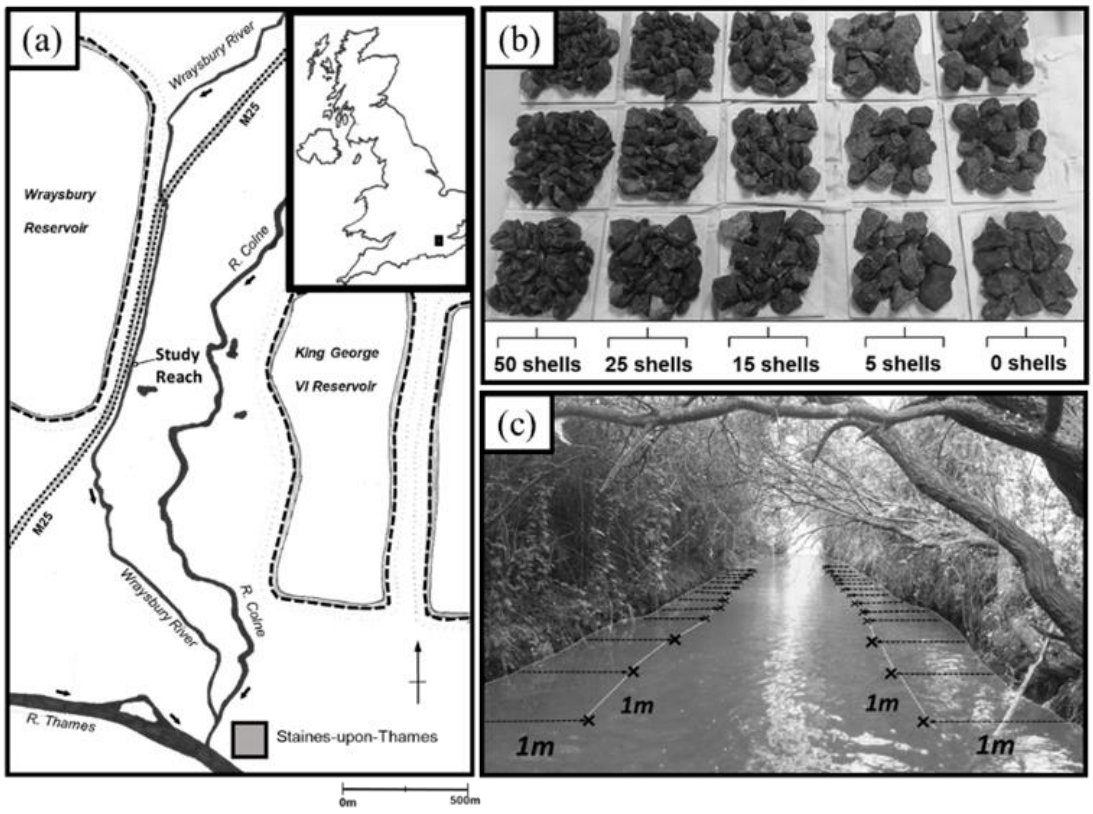


Figure 3.1 (a) Location of the Wraysbury River (Lat 51.45225; Long -0.520528) with labelled study reach; (b) a series of manipulated substrate tiles photographed and arranged by shell treatment categories; (c) a photograph of the study reach (Lat 51.451842; Long -0.520814) with annotations demonstrating substrate tile deployment positions.

Experimental Design

Our substrate tiles were designed to identical specification before gradated treatments of *D. r. bugensis* shells were added to their surface. A series of coarse pebbles (40-60mm on *a*-axis)

were firstly collected by hand from Wraysbury River, washed and oven dried in the laboratory (6hrs; 400^{o}C). 20 pebbles were then randomly selected and glued with silicon aquarium sealer onto a 150 x 150mm patio tile base. The structural arrangement of clasts on each tile covered all of its surface and clast edges overlapped, leaving minor interstices between each pebble. Twenty-five substrate tiles were constructed for each of three experiments.

For substrate tile shell treatments, adult *D. r. bugensis* specimens (24-30mm shell length) were collected from a known site on the Wraysbury River (Lat 51.455889; Long -0.518917) before removal of all inner-shell animal tissue through boiling and extraction using forceps. For each specimen, shell valves were glued back together with aquarium sealant in analogue appearance to a live animal. Analogue mussels (each containing two shell valves) were then glued to the surface of our substrate tiles at numbers of 50, 25, 15, 5 or 0 per substrate, or 2220, 1111, 666, 222 and 0 *D. r. bugensis* individuals m^{-2} of tile, respectively (**Figure 3.1b**). For comparative purposes, mean density of *D. r. bugensis* recorded in the Wraysbury River, c.10m upstream of the study reach, during the same period of time was ~200 individuals m^{-2} (Mills 2017, unpublished), roughly equivalent to our lowest 5 shell substrate treatment.

Five replicates of each shell density were used for each of three experiments (substrate tile n = 25 x 3) with the 0 shell treatment acting as control. Care was taken to ensure *D. r. bugensis* shells were glued to our substrate tiles by their posterior keel and orientated in a randomised direction; simulating field observations of live mussels in the Wraysbury River. For higher treatment densities (e.g. 50, 25 shells), complex interstices were formed between shell individuals and the substrate tile appearance strongly resembled that of a natural mussel bed or druse. With the lower shell treatments (15, 5 shells), coverage on the substrate tiles was sparser and care was taken to ensure that glued individuals were approximately equidistant (**Figure 3.1b**).

Substrate tiles were deployed at the study site for the first experiment between 30th June - 30th July 2017 (30 days), second experiment between 30th July – 30th September 2017 (62 days) and third experiment between 30th September – 15th October 2017 (14 days). The deployment periods of our experiments were staggered due to limited space and availability of homogenous transects within the Wraysbury River. In conducting tests of different length, we hoped to evaluate effects of substrate deployment duration on the density and taxonomic richness of colonising invertebrates. Across other environments, artificial substrates have appeared to achieve stabilised invertebrate communities within 30-60 days (Roby et al. 1978; Meier et al. 1979; Boothroyd and Dickie 1989) or occasionally, shorter periods (e.g. 19 days; Wise and Molles 1978 and 14 days; Figueroa et al. 2006). We thought comparison of experiments across similar time frames would help guide future study using our approach.

In each case, 25 substrate tiles were constructed, labelled and transported to the study reach for deployment on the first day of the test duration. Here they were placed in the stream 1m from the wetted bank and 1m equidistant, in randomised order (**Figure 3.1c**). Particularly coarse pebbles and cobbles had to be occasionally removed from the stream bed immediately underneath some substrate tiles; ensuring flattened elevation and increased stability in situ. In no cases was stream flow velocity sufficient to dislodge or transport any substrate tile during deployment.

At the start of each experiment, stream flow and various physicochemical parameters were measured with samples at 0.6 depth above the deployment location of each substrate tile. Parameters included stream pH, dissolved oxygen (DO; mg L^{-1}), conductivity (µs cm^{-1}), temperature (^{o}C) and depth (cm). Aside from depth, all were recorded using a HACH™ HQ30d multi-probe and HI9811-5N pH/EC/TDS/°C portable meter. Stream flow measurements were also taken using a Valeport electromagnetic flow meter (model 801) using a 30 second-average

velocity function. These measurements were conducted to record variability in stream conditions between substrate deployment locations per experiment.

On the last day of each experiment's deployment period (after 14, 30 and 62 days, respectively), colonised invertebrate communities were sampled from the substrate tiles in-stream. In all cases, a surber sampler net (mesh size 250 μm^{-1}) was lowered by hand to the stream bed to envelop the surface of the deployed substrate tile. The substrate tile was then carefully loosened from the bed and lifted from the stream inside the covering net. The contained substrate tile and netting were thoroughly washed in a basin on the river bank and inspected carefully for attached invertebrates. Mineral and biological material washed and picked from each substrate tile was collected in a 180 μm^{-1} mesh field-sieve before preservation in a labelled 50 ml polyethene vial using Industrial Methylated Spirit (90%).

In the laboratory, all invertebrates per sample were enumerated and identified under a high power ocular microscope. Identification was made to species level except for *Simulium* spp., Oligochaeta spp., and the family Chironomidae (identified to tribe). Individuals of Limnephilidae spp. and Hydropsychidae spp. were also grouped at family level due to morphological ambiguity at their smallest size-ranges.

Data Analysis

For each substrate tile and corresponding shell treatment, invertebrate density (individuals m^{-2}) and taxon richness was calculated. Graphical summaries of invertebrate richness and the contribution of different taxonomic orders to mean total density per treatment were made, including: Amphipoda spp., Coleoptera spp., Diptera spp. Trichoptera spp., Ephemeroptera spp., Gastropoda spp., and Bivalva spp.. Following this, we conducted two-way ANOVAs on mean invertebrate density and richness using shell substrate treatment and experiment duration category as factors. This was undertaken to assess the impact of shell treatments across all

experiments, ensuring no interactions between experiment duration and shell density effects. For invertebrate density, data were natural-log transformed to meet parametric assumptions prior to analysis. Where significant differences were found across levels of shell substrate treatment or experiment length; *post hoc* multiple comparison procedures were undertaken using the Holm-Sidak method. To test for variation in invertebrate density and richness within experiments; we also conducted one-way ANOVAs between shell treatments per experiment. Where there was significant variation between shell treatments, *post hoc* pairwise comparisons were undertaken using a Tukey test. All calculations were made using Sigmaplot 13.0 (Systat Software, Chicago, Illinois, USA).

Ordinations of community structure were performed with statistical software package PRIMER-E Ltd. 2009 (Clarke 1993; Clarke and Warwick 2001; Clarke and Gorley 2006). Across all experiments, Non-Metric Multidimensional Scaling (NMDS) based on Bray-Curtis dissimilarities was used to assess community composition per shell treatment based on mean invertebrate density (individuals m^{-2}) per taxon. Prior to statistical analysis, all data were Log(X+1) transformed to moderate for the effects of rare or highly abundant taxa (Clarke and Green 1988; Legendre and Gallagher 2001) and all taxa accounting for less than 0.5% of total mean density per experiment were excluded to reduce distortion of assemblage differences. NMDS is a widely used approach for displaying invertebrate community structure data (e.g. Barquín and Death 2004; Wikström and Kautsky 2007; Herbst et al. 2012).

Results

Measurements suggested strong homogeneity of physicochemical conditions above deployed substrates at the start of each experiment. Parameters, including stream dissolved oxygen (mg L^{-1}), pH, conductivity (µs cm^{-1}), temperature (^{o}C), flow rate (m s^{-1}) and depth (cm) presented a small range of mean values with very low standard error (**Table 3.1**). Within experiments, one-

way ANOVAs between shell substrate treatments failed to detect significant differences for any parameter. Across all experiments, the range of mean values for stream dissolved oxygen, pH, conductivity, temperature, flow and depth suggested minor physicochemical differences at the start date of each experiment (**Table 3.1**). This was expected due to seasonal environmental variation, which will be discussed further in the context of our results.

Table 3.1 Summary of physicochemical measurements sampled above deployed substrate tiles, including: stream dissolved oxygen (m g^{-1}), pH, conductivity (µS cm^{-1}), temperature (^{o}C), flow (m S^{-1}) and depth (cm). Table shows the range, mean and standard error of each parameter for all measurements per experiment. Also shown: results of one-way ANOVA for parameter values between substrate *D. r. bugensis* shell treatments per experiment.

	Parameter Measured	Range *all samples*	Mean *all samples*	SE	ANOVA *(between substrate shell treatments)* Test	*p*- value
14 day experiment	***Dissolved oxygen*** **mg L^{-1}**	9.4 - 9.8	9.6	0.02	$F(4, 20) = 2.9$	0.878
	pH	8.02 - 8.05	8.0	0.002	$H = 1.2(4)$	0.884
	Conductivity **µS cm^{-1}**	810 - 811	810	0.07	$H = 2.2(4)$	0.702
	Temp **^{o}C**	17.32 - 17.35	17.35	0.002	$H = 2.8(4)$	0.59
	Flow **m S^{-1}**	0.2 - 0.3	0.25	0.003	$F(4, 20) = 0.1$	0.99
	Stream depth **cm**	28 - 35	31.3	0.36	$F(4, 20) = 1.5$	0.23
30 day experiment	***Dissolved oxygen*** **mg L^{-1}**	8.5 - 9.0	8.6	0.02	$F(4, 20) = 0.6$	0.65
	pH	8.02 - 8.03	8.0	0.001	$F(4, 20) = 1.0$	0.431
	Conductivity **µS cm^{-1}**	891 - 892	891	0.07	$H = 5.8(4)$	0.213
	Temp **^{o}C**	17.09 - 17.13	17.10	0.003	$F(4, 20) = 7.4$	0.578
	Flow **m S^{-1}**	0.2 - 0.3	0.27	0.01	$H = 6.1(4)$	0.962
	Stream depth **cm**	27 - 31	29.4	0.46	$F(4, 20) = 2.9$	0.884
62 day experiment	***Dissolved oxygen*** **mg L^{-1}**	8.7 - 9.3	8.9	0.03	$F(4, 20) = 2.4$	0.085
	pH	7.95 -7.98	8.0	0.002	$F(4, 20) = 0.7$	0.616
	Conductivity **µS cm^{-1}**	871 - 873	810	0.07	$H = 0.2(4)$	0.993
	Temp **^{o}C**	18.13 - 18.15	18.14	0.001	$F(4, 20) = 0.5$	0.722
	Flow **m S^{-1}**	0.2 - 0.4	0.35	0.02	$F(4, 20) = 0.4$	0.838
	Stream depth **cm**	27 - 34	32.2	0.47	$F(4, 20) = 2.4$	0.083

A total of 4826 invertebrate individuals were identified on substrate tiles across all experiments, including 44 taxa. For each case, the three most abundant groups found were amphipod shrimps of Gammaridae, riffle beetles of Elmidae and non-biting midges of

Chironomidae. The net spinning caddis family Hydropsychidae was the fourth most abundant group for both 30 day and 62 day experiments, but it was *Oligochaeta* spp. for the 14 day experiment (**Appendix II** 269 pp.). While nearly all recorded invertebrates were native, several invasive species were found at low density across experiments, including *Crangonyx pseudogracilis* (Bousfield, 1958), *Dikerogammarus haemobaphes* (Eichwald, 1841), *Potamopyrgus antipodarum* (Gray, 1843) and *D. r. bugensis* (**Appendix II**; 268 pp.).

Mean invertebrate density was highest for the 50 shell treatment and lowest on the control in all three experiments (**Figure 3.2**). With two-way ANOVA, significant differences in mean invertebrate density (*Ln*-transformed) were found among substrate shell treatments. In *post hoc* Holm-Sidak tests, the 50 shell treatments presented significantly higher invertebrate density compared to all others. In addition, the moderate 15 and 25 shell substrate treatments showed significantly higher density compared to the no-shell controls. For this test we found no significant interactions between experiment duration and shell density effects (**Table 3.2**).

Table 3.2 Results of two-way ANOVA for mean invertebrate density (individuals m^{-2}) and taxonomic richness using substrate tile shell treatment and experiment duration category as factors. For invertebrate density, data were natural-log transformed to meet parametric assumptions prior to analysis.

Parameter	Source of Variation	DF	SS	MS	F	P	Holm-Sidak Test
Mean invertebrate Density (m^{-2}) ± SE	*Substrate tile shell treatement*	4	5.81	1.45	17.3	**<0.001*** **	50 > all; 25, 15 > Cont.
	Experiment duration	2	3.15	1.58	18.8	**<0.001*** **	30d > 62d, 14d; 62d > 14d
	Subs. treatment x experiment dur.	8	0.35	0.04	0.5	0.832	
	Residual	60	5.04	0.08			
	Total	74	14.35	0.00			
Mean invertebrate Richness ± SE	*Substrate tile shell treatement*	4	131.01	32.75	8.6	**<0.001*** **	50 > 5; 50, 25, 15 > Cont.
	Experiment duration	2	244.16	122.08	32.0	**<0.001*** **	30d, 62d > 14d
	Subs. treatment x experiment dur.	8	39.31	4.91	1.3	0.267	
	Residual	60	228.80	3.81			
	Total	74	643.28	8.69			

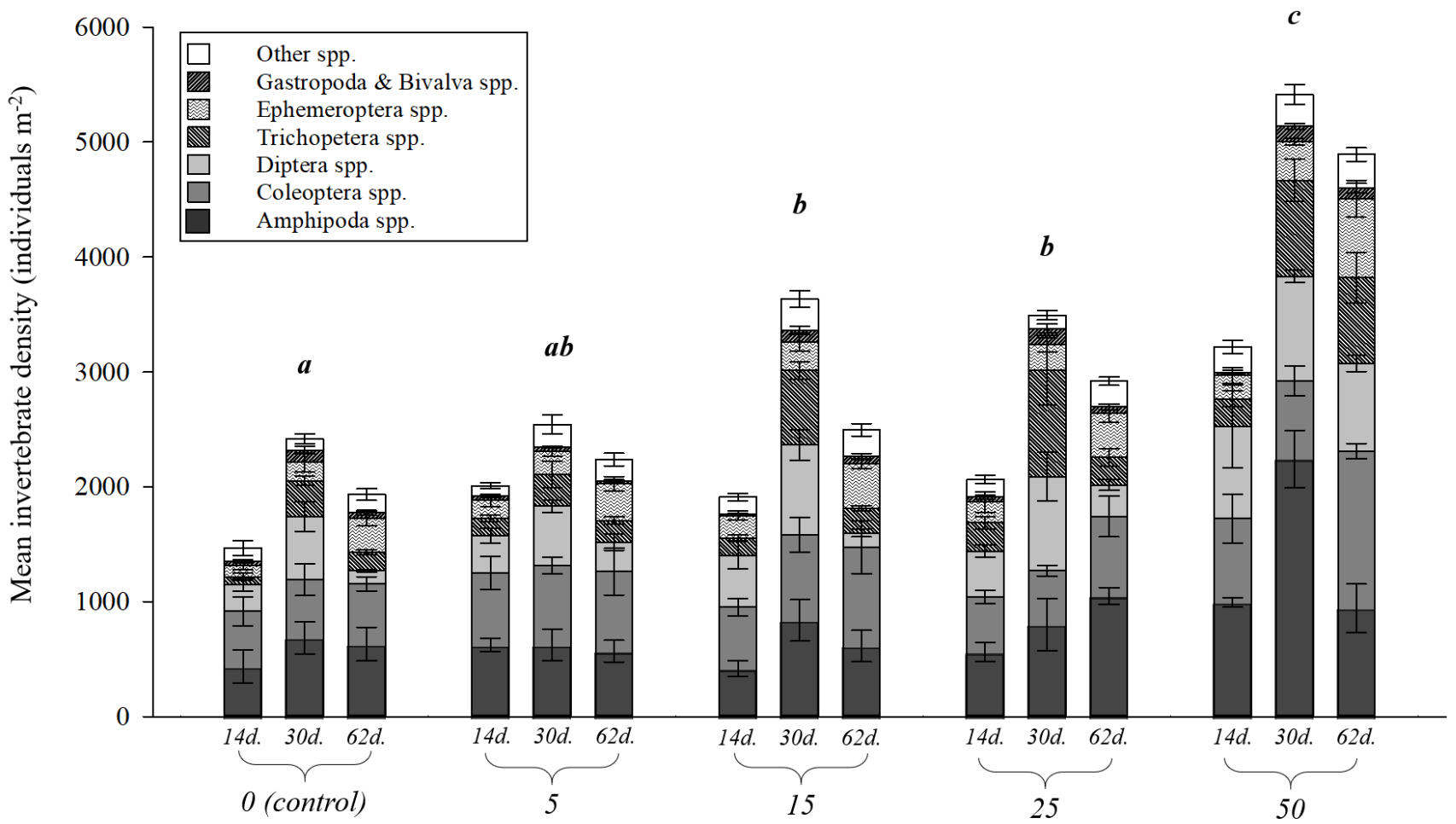


Figure 3.2 Proportional contribution of different taxa groups to total mean invertebrate density (individuals m^{-2}) across substrate tile shell treatments for all experiment duration categories. Error bars show standard error. Symbols denote significant differences between substrate treatment categories after allowing for effects of experiment duration category according to two-way ANOVA (p = <0.001).

Within experiments, one-way ANOVA presented significant differences in invertebrate density between treatments for all tests. According to post-hoc Tukey's procedures, the 50 shell treatment had significantly higher mean density than all others in the 30 and 62 day experiments. For the 14 day test, the 50 shell treatment was the only one significantly higher than the control (**Table 3.3**).

Table 3.3 Mean invertebrate density (individuals m^{-2}) and taxonomic richness for D. r. bugensis shell treatments per manipulated substrate tile exposure period (± SE). Results from one-way ANOVA and Tukey's tests are also presented per experiment (denoted by exposure period) with significant values in bold.

Parameter	Deployment Period	Artificial substrate shell density					ANOVA		Tukey test
		0 (cont.)	5	15	25	50	Test	*p*- value	
Mean invertebrate Density (m^{-2}) ± SE	*14 days* (Ln)	1467 ± 293	2009 ± 155	1911 ± 173	2062 ± 83	**3217 ± 640**	$F_{(4, 20)} = 3.8$	0.019*	50 > 0
	30 days	2418 ± 318	2542 ± 199	3635 ± 406	3475 ± 584	**5413 ± 443**	$F_{(4, 20)} = 8.6$	<0.001***	50 > 0, 5, 15, 25
	62 days (Ln)	1982 ± 138	2319 ± 167	2586 ± 424	2941 ± 365	**4915 ± 510**	$F_{(4, 20)} = 9.8$	<0.001***	50 > 0, 5, 15, 25
Mean invertebrate Richness ± SE	*14 days*	9.0 ± 0.8	10.2 ± 1	12.4 ± 0.5	12.2 ± 0.7	12.0 ± 1.5	$F_{(4, 20)} = 2.3$	0.099	N/A
	30 days	14.0 ± 0.6	13.6 ± 0.5	16.4 ± 0.5	16.0 ± 1.1	**17.0 ± 0.6**	$F_{(4, 20)} = 4.4$	0.011*	50 > 5
	62 days	11.2 ± 0.7	**15.2 ± 1.0**	14.0 ± 0.4	14.8 ± 0.7	**16.6 ± 1.3**	$F_{(4, 20)} = 5.2$	0.005**	50 > 0, & 5 > 0

Taxa groups contributing to total invertebrate density appeared consistent between experiments and across shell treatments, but for some exceptions. In the 30 day experiment, Amphipoda spp., showed a higher percent contribution to total density for the 50 shell treatment (41%) compared to others (23-28%). Similarly for the 62 day experiment, Trichoptera spp. (50 shell treatment; 15%, others 8-11%) and Diptera spp. (50 shell treatment; 16%, others 5-11%) were more dominant contributors to the 50 shell treatment. Within the 14 day experiment, proportional contributions of taxa groups appeared more homogenous throughout treatments. Notably in this case, total density appeared consistently lower across treatments than for the 30 and 62 day tests (**Figure 3.2**).

With two-way ANOVA, significant differences in mean total invertebrate density (*Ln*-transformed) were found according to experiment duration category, after allowing for

differences in substrate shell treatment. In Holm-Sidak tests, the 14 day experiment presented strongly significant, lower invertebrate densities compared to both others **Table 3.2** The 30 day experiment also presented higher densities compared to the 62 day experiment, but at weaker significance.

Mean invertebrate richness was highest for the 50 shell treatment in the 30 and 62 day experiments and for the 15 shell treatment in the 14 day experiment (**Figure 3.3**). According to two-way ANOVA, significant differences in richness were found between substrate shell treatments, after allowing for experiment duration category. In Holm-Sidak tests, control treatments (0 shells) presented significantly lower invertebrate richness compared to all others except for the 5 shell treatment. The latter was also significantly lower than the 50 shell treatment. For this test we again found no significant interactions between experiment duration and shell density effects (**Table 3.2)**.

Within experiments, one-way ANOVA also presented significant variability of richness between treatments; though only in the 30 and 62 day experiments. Tukey's tests showed that in the 30 day test, richness was significantly higher for the 50 shell treatment compared to the 5 shell treatment. For the 62 day test, the 50 shell treatment was significantly higher than the control **(Table 3.3**).

In general, mean richness appeared lower across treatments in the 14 day experiment when compared to equivalents in the 30 and 62 day tests (**Figure 3.3**). With two-way ANOVA, significant differences in richness were found according to experiment duration category, after allowing for differences in substrate shell treatment. In Holm-Sidak tests, the 14 day experiment presented significantly lower invertebrate richness compared to both others (**Table 3.3**) but there was no significant difference between the the 30 and 62 day tests.

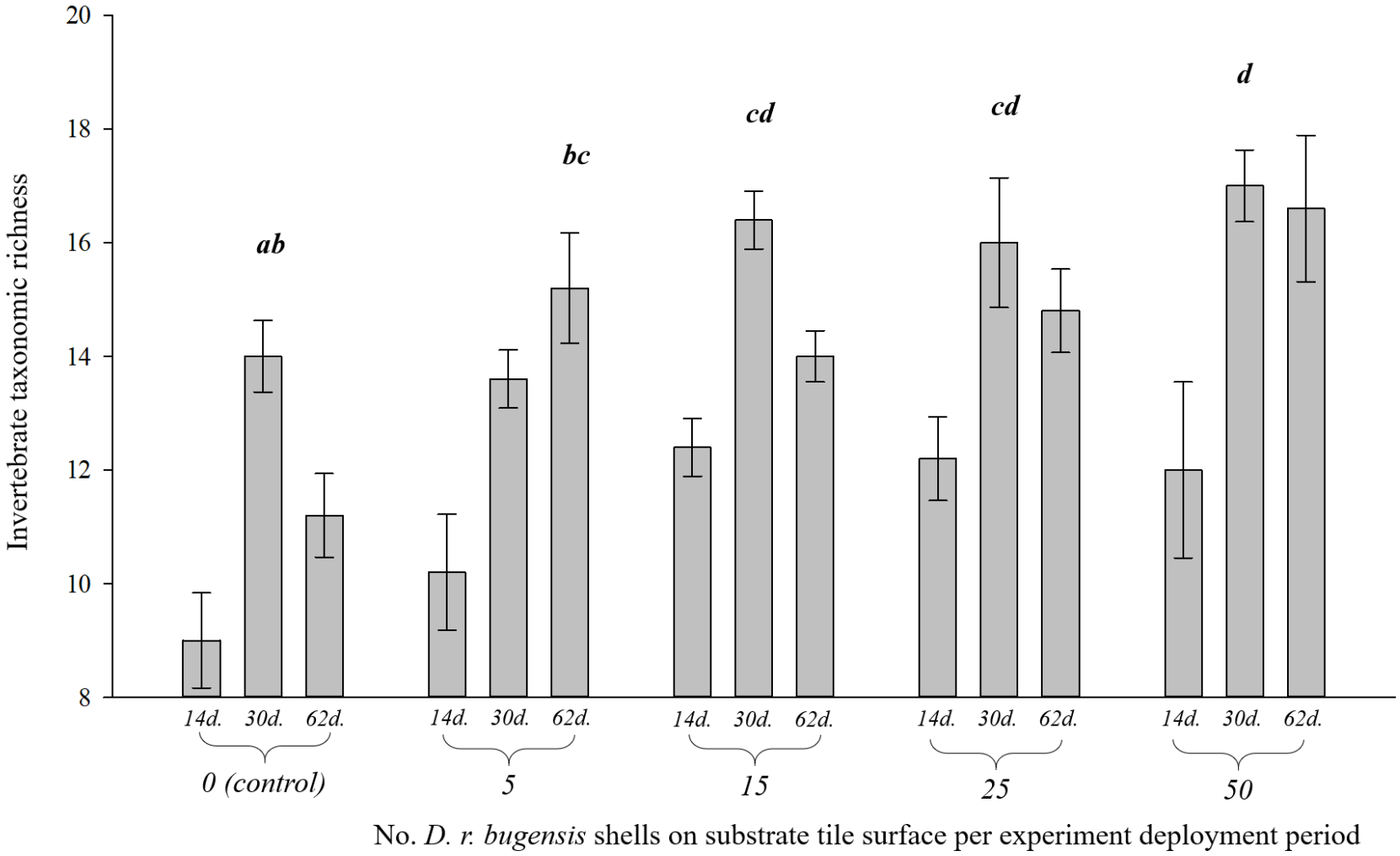


Figure 3.3 Mean invertebrate richness across substrate tile shell treatments for all experiments. Error bars denote standard error. Symbols denote significant differences between substrate treatment categories after allowing for effects of experiment duration category according to two-way ANOVA ($p = <0.001$)

In the NMDS plot (stress 0.05), mean community composition across experiments (driven by taxa contributions to total invertebrate density) appeared most segregated by experiment rather than shell treatment (**Figure 3.4**). For the 62 day experiment, the three highest shell treatments were closely grouped together and more distanced in the plot from their respective lower treatments. Similarly, the highest two shell treatments in the 30 day experiment were closely grouped and separated from their respective lower shell treatments. In contrast, the 14 day experiment presented closer association between the lower three treatments, while the remaining higher treatments appeared more isolated on the plot.

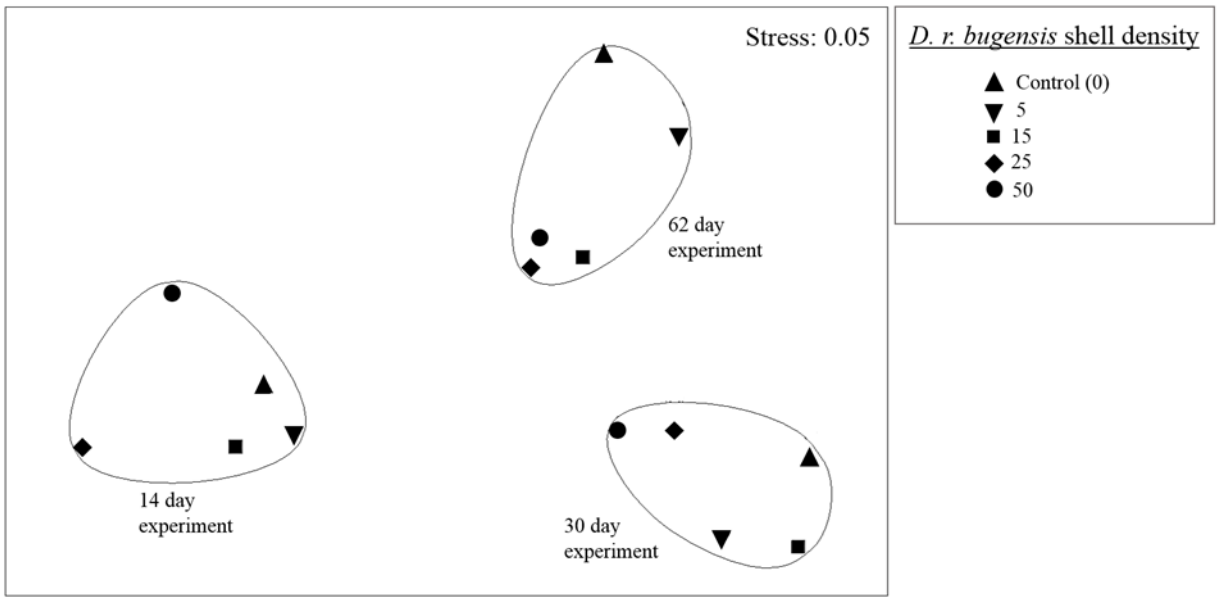


Figure 3.4 Non-metric Multi-dimensional Scaling (NMDS) ordinations of Bray-Curtis similarities in community structure (based on proportion of taxa contribution to total invertebrate density) for each substrate treatment per experiment.

Discussion

The response of invertebrates to substrate tile treatments complimented facilitative associations of invasive *Driessena* spp. (e.g. Stewart and Haynes 1994; Kuhns and Berg 1999; Ward and Ricciardi 2007; Ozersky et al. 2011). For example, the largest mean increase of invertebrate density was consistently found between the control and highest substrate shell categories (14 day: 119%, 30 day: 124%, 62 day: 148%); with these treatments driving significant variation both within and across experiments. Given homogenous physicochemical conditions for substrate tiles *in situ*; we could attribute this variation to differences in *D. r. bugensis* shell densities. Such effects were expected because invertebrates have shown positive responses to the physical structure of shells (Botts et al. 1996; Hovarth 1999).

Dominant taxa in this study, including the riffle beetle *Elmis aenea*, caddisfly *Hydropsyche* spp., and shimp *Gammarus pulex* were consistently found at increased densities on higher substrate shell treatments and feasibly benefitted from effects provided. For *E. aenea*, the taxon's size permits flow refuge by exploitation of small interstices (Peris et al. 2015) characteristic of *Dreissena* spp. mussel beds. With *Hydropsyche* spp., shells may provide protrusive bed features on which nets and tubular refuges are constructed for suspension feeding (Edington 1968). For *G. pulex*, shell structures may provide predator refugia, as suggested during *ex-situ* laboratory experiments on *Dreissena* spp. (Reed et al. 2004; Kobak et al. 2014). In all cases, taxa could benefit from increased habitable surface area, as associated with natural *Dreissena* spp. beds (Ricciardi et al. 1997; Stewart et al. 1998; Ward and Ricciardi 2007).

Such physical traits have also explained the positive response of invertebrate richness to invading *Dreissena* spp. (Griffiths 1993; Stewart and Haynes 1994; Ricciardi 2003), which was similarly correlated with the higher substrate shell treatments in our study. Across

experiments, significant variation between treatments was driven by low and high richness values for the control and highest shell categories, respectively. This was similar to trends for invertebrate density, however the response of richness appeared reduced. In particular, significant differences within experiments were only found between treatments for the 30 and 62 day tests; alongside weaker *p* values than for density. Viewing too, comparatively lower richness values throughout the 14 day experiment, this test appeared subject to different colonisation effects than the other experiments.

One possibility was that methodologically, 14 days was an insufficient duration for colonising invertebrates to achieve taxonomic richness representative of shell treatment effects. Artificial substrates are typically saturated by invertebrates to stabilised richness within 30 – 60 days (Roby et al. 1978; Meier et al. 1979; Boothroyd and Dickie 1989) despite variation across sampling methodologies and geographical regions of deployment (Boothroyd and Dickie 1989). While some research suggests shorter durations are sufficient for representative assemblages to appear (e.g. 19 days; Wise and Molles 1978 and 14 days; Figueroa et al. 2006); this study found that significant variation in richness between experiments, after allowing for effects of substrate shell treatment, was driven only by lower values for the 14 day experiment. This suggested temporal factors were of importance to our methodology.

Aside from substrate deployment length; the timing of each test, though seasonally proximate, was also different (particularly comparing the 30 and 14 day experiment). This could mean invertebrate life histories, such as the pupation or emergence of adult insects, prevented important taxa groups from achieving comparable assemblages across tests. For example, Trichoptera spp. found in the longer two experiments, but not in the 14 day test, included *Goera pilosa* (Fabricus, 1775), *Brachycentrus subnubilis* (Curtis, 1834) and *Limnephilus lunatus* (Curtis, 1834). Given the diversity of life history patterns shown by such taxa (Meier et al. 1979; Jannot et al. 2008), their colonisation could have been restricted at this time compared

to others. Generally, seasonal shifts in stream primary production or autochthonous inputs would also be expected in temperate streams (e.g. Roby et al. 1978; Hawkins and Sedell 1981); causing variation in food availability to impact invertebrate distribution and life history patterns (Vannote et al. 1980; Jannot et al. 2008). In our study, distinct community compositions within experiments, identified in the NDMS plot, could have been due to such factors; although they remain difficult to isolate from effects of experiment duration.

In evaluating the experiment methodology, the issues of substrate deployment time and seasonal period should be more carefully standardised in future experiments. Chiefly, substrate deployment of 30 days or longer, during consistent seasonal periods could be used for achieving more comparable results between experiments. Where experiments of different duration are conducted, simultaneous start times could also be employed; given sufficient homogenous space for deployment. However, we argue our current study still provides a useful benchmark for potential impacts of *D. r. bugensis* in Wraysbury River. A significant, positive response of invertebrate density and richness was clearly shown across experiments, despite differently timed deployment periods. At particular population levels (between 1110 and 2220 individuals m^{-2}), we may conclude *D. r. bugensis* would significantly impact benthic community structure in this system. Considering the likelihood *D. r. bugensis* would reach such densities, we may comment whether such impacts would feasibly occur in future.

In this regard, there remains uncertainty regarding potential invasiveness of *D. r. bugensis* in environments like the Wraysbury River. Initial establishment of the species at this site was considered surprising (Aldridge et al. 2014) and the majority of high density, invasive populations have been found in deep, lentic environments of North America. For example, 16, 000 individuals m^{-2} (Lake Michigan; Nalepa et al. 2009), 75, 000 individuals m^{-2} (Lake Huron; Nalepa et al. 1995) and 342, 000 individuals m^{-2} (Lake Erie; Howell et al. 1996). In more illuminated, shallow systems, *Dreissena* spp. are vulnerable to visual predation by waterfowl

and fish (Karatayev et al. 1997; Petrie and Knapton 1999; Haynes et al. 1999), while early-stage larval veligers exhibit higher mortality with increased exposure to ultraviolet radiation (Thaw et al. 2014) and flow turbulence (Hovarth and Lamberti 1999; Rehmann et al. 2003). In Wraysbury River, such limitations could prevent *D. r. bugensis* populations increasing from the modest densities currently recorded (maximum: 198 individuals m^{-2}; Mills 2017, unpublished). We suggest clear impacts of *D. r. bugensis* on cohabiting invertebrate communities would be unlikely to occur in current conditions.

However, the fact we used analogue *D. r. bugensis* rather than live mussels should be noted. While comparative studies of invertebrate communities on live and dead *Dreissena* spp. suggest invertebrates primarily respond to the physical structure of shells (Botts et al. 1996; Hovarth 1999); specific effects of live *D. r. bugensis* may provide further benefits for some taxa. In particular, *D. r. bugensis* suspension feeding of phytoplankton and subsequent pseudofaces excretion has been shown to concentrate phytic biomass, nutrients and minerals on the bed (Izvekova and Lvova-Katchnanova 1972; Stewart and Haynes 1994). Such materials may be consumed by invertebrates (e.g. MacIsaac 1995; Pace 1998) or encourage the development of biofilm and submersed macrophytes (Arnott and Vanni 1996; Stoeckmann and Garton 2011); providing additional food sources and greater habitat heterogeneity. In particular, the facilitation of Chironomidae spp. by *Dreissena* spp. has been associated with consumption of pseudofaeces (Griffiths 1993; Botts et al. 1996); another prominent group found in our study. We would expect even stronger facilitation of such taxa when colonising equivalent populations of live mussels.

In describing our findings in the context of invasive species management, we hope not to overstate the potentially positive, facilitative impacts of *D. r. bugensis* on cohabiting invertebrate communities. Over annual time periods, invasive *Dreissena* spp. have been associated with periodic desaturation of dissolved oxygen in North American rivers due to

population respiration demand (Effler and Siegfried 1994; Effler et al. 1996; Caraco et al. 2000). In poorly aerated systems, resulting anoxia may degrade, rather than facilitate faunal diversity and richness (Effler et al. 1996), including vertebrate groups such as fish. In addition, research in other invaded environments have shown initial benthic responses to *Dreissena* spp. weaken after several years (*Sensu* Strayer and Malcom 2006; Karatayev et al. 2015); possibly driven by developing predatory regulation of invertebrates by fish (Karatayev et al. 1997; Haynes et al. 1999). In Wraysbury River and other UK environments, such effects could be driven by widespread benthiverous species like bullhead *Cottus gobio* (Linnaeus 1758) and gudgeon *Gobio gobio* (Linnaeus 1758). Outwardly positive effects of *D. r. bugensis* for benthic fauna in UK rivers may be similarly unsustainable and decline over time.

Further, facilitative impacts of *D. r. bugensis* may allow other invasive invertebrates, including several Ponto-Caspian taxa, to benefit from *D. r. bugensis* proliferation in the UK (Gallardo and Aldridge 2013; Gallardo and Aldridge 2015). For example, invasive, predatory amphipods of *Dikerogammarus* spp. have been shown to present an affinity to *Dreissena* spp. shells (Kobak and Żytkowicz 2007) and like other taxa, benefit from increased habitat complexity provided by mussel beds (Gallardo and Aldridge 2013). Interestingly, in both our 30 and 62 day experiments, invasive shrimp *Dikerogammarus haemobaphes* (Eichwald, 1841) was explicitly identified on our higher shell treatments. While found at low abundance, this was our first record of a Ponto-Caspian shrimp for the Wraysbury River after approximately three years of recent study. While the possibility *D. r. bugensis* may facilitate other Ponto-Caspians in Wraysbury River can only be highlighted and not conclusively demonstrated here; additional research might examine such interactions further and progress understanding on the implications of *D. r. bugensis* establishment in UK rivers.

Conclusions

In three colonisation experiments with manipulated substrate tiles, significantly higher invertebrate density was found with increasing *D. r. bugensis* shell treatment. Prominent taxa found at greater density with higher shell treatments included amphipod *G. pulex*, riffle beetle Elmidae spp., net spinning caddis *Hydropsyche* spp. and dipteran Chronomidae spp.. Increasing shell treatments may have provided more habitable surface area, predator and flow refugia for invertebrates alongside facilitation of feeding strategies for certain taxa.

Positive responses of invertebrate taxonomic richness was also found with higher *D. r. bugensis* shell treatment; though weaker than for invertebrate density. Within experiments, significantly increased richness with higher shell treatments occurred only for the longer, 30 and 62 day experiments. Our shortest, 14 day experiment presented comparably homogenous richness values between shell treatments.

Given evidence of similar physicochemical conditions between experiments; less clear variation in richness and density across treatments for the 14 day test could have been driven by insufficient substrate deployment duration for stabilised invertebrate communities to develop. Further, experiments were not performed concurrently and seasonal change may have impacted invertebrate responses. In evaluating our methodology for future study; substrate deployment of 30 days or longer, during consistent seasonal periods was recommended.

Despite differences in experiment duration and timing, we observed consistent, significantly increased invertebrate density and richness across the highest substrate shell treatments, equivalent to 2220 *D. r. bugensis* individuals m^{-2}. If similar mussel densities developed in the Wraysbury River, we would expect comparable impacts on benthic fauna to occur. The feasibility of such populations occurring in this site appears low, however our results may be conservative, failing to account for additional impacts of live mussels.

In the context of invasive species management, potential facilitation of benthic fauna by *D. r. bugensis* in Wraysbury River was not considered particularly positively, nor sustainable. In other invaded regions, *Dreissena* spp. have been associated with periodic stream anoxia and other feedbacks which may degrade aquatic communities. Further, facilitative effects on the benthos may assist the establishment of other invasive invertebrates such as amphipods of *Dikerogammarus* spp., first recorded in the Wraysbury River during this study.

Part 2: Impact Mechanisms

Post-invasion impacts of D. r. bugensis on macroinvertebrate community structure in a UK river.

Chapter 4: *Flume experiments investigating geomorphic impacts of invasive quagga mussel (Dreissena bugensis rostriformis, Bivalva: Dreissenidae) in rivers.*

Summary:

As drivers of fluvial geomorphic processes, certain aquatic organisms may be important to the morphological and biological structure of rivers. While currently understudied, the epifaunal, invasive bivalve mollusc *Dreissena rostriformis bugensis*, known as the 'quagga mussel' could hold significant geomorphic agency in rivers. Given field observations of *D. r. bugensis* in a gravel bed UK river, it was hypothesised their populations could alter stream sediment flux and flow hydraulics through byssus-substrate connections and the physical structure of mussel beds. To test this, *ex-situ* flume experiments were conducted to investigate whether *D. r. bugensis*, under simulated river conditions, could alter bedload transport rates and near bed stream velocities. The first experiment assessed bedload transport from a test bed of graded fluvial gravels treated to various densities of *D. r. bugensis*. Flume conditions were manipulated to exceed stream velocities critical for particle entrainment over a series of hourly experimental runs. Runs with mussel densities equivilant to 250 individuals m^{-2} were associated with significantly reduced mean bedload transport rates compared to those with densities of 125 individuals m^{-2} and control tests with no mussels. A second experiment investigated near bed flow velocities and stream Turbulent Kinetic Energy (TKE) 0-5cm above a similar test bed of graded fluvial gravels, treated again to the same densities of *D. r. bugensis*. In this experiment, the test bed was subjected to normal flow velocities, analagous to mean hydraulic conditions in an invaded UK river (approx. 0.2 m s^{-1}). Over a series of experimental runs per *D. r. bugensis* treatment, flow velocity and TKE depth profiles were constructed at three positions above the test bed using Acoustic Doppler Velocimeter (ADV) measurements. For two out of three profiles, mussel densities equivalent to 250 individuals m^{-2} were consistently associated with significantly reduced near bed flow velocities compared to those with with densities of 125 individuals m^{-2} and control tests with no mussels. Trends for TKE were less clear, however the higher *D. r. bugensis* treatment generally presented more turbulent near bed flows compared to others. Both experiments raise the possibility that *D. r. bugensis* may be a geomorphic agent where established in rivers. This could have structuring impacts for cohabiting ecology within the invaded UK range and represents a previously unstudied mechanism of *D. r. bugensis* impacts. Despite clear limitations of ex-situ study, experiments herein provide a benchmark for understanding fluvial geomorphic impacts of *D. r. bugensis*. Additional work could replicate tests with different mussel densities, benthic species mixtures, bed grain sizes, hydraulic flow regimes and flume channel dimensions.

Introduction

Aquatic organisms can drive fluvial geomorphic processes by altering bed stability and stream hydraulics (Jumars & Nowell 1984; Fei et al. 2014, Rice et al. 2016). While knowledge on their geomorphic agency remains limited, impacts of certain taxa groups have been suggested (Johnson et al. 2011; Pledger et al. 2014). For example, stream sediment flux may be altered by bed destabilisation from fish foraging (Pledger et al. 2014; Pledger et al. 2016), nesting (Kondolf et al. 1993; Hassan et al. 2008) and crayfish burrowing (Vaughn & Hakenkamp 2001; Statzner et al. 2000; Zimmerman et al. 2007; Johnson et al. 2011); alongside bed stabilisation from caddisfly net-spinning (Statzner et al. 1999; Cardinale et al. 2004), pupal-case building (Statzner 2012), biofilm adhesion ((De Brouwer et al. 2005; Vignaga et al. 2013) and macrophyte rooting (Abernethy and Rutherford 2000; Micheli and Kirchner 2002). Stream hydraulics may be altered due to changes in bed roughness driven by the presence of mussel beds (Frostick et al. 2014) benthic mosses (Nikora et al. 2003), plant stems (Widdows et al. 2008), submersed macrophytes (Sand-Jensen 1998; Schulz et al. 2003; Kleeberg et al. 2010) and large woody debris (Abbe and Montgomery 1996). These organisms and features can attenuate stream velocities, cause turbulent flows and drive secondary impacts on sediment flux (e.g. Lamarre and Roy 2004; Rickenmann et al. 2011). Such dynamics are important to wider morphological and biological structuring of rivers (Rice et al. 2016); though further investigations are needed to elucidate impacts of understudied taxa, especially invasive species (Harvey et al. 2011; Fei al. 2014).

Since the pioneering work of Elton (Elton 1958), impacts of invasive species have been part of scientific and public discourse (Pfeiffer & Voeks 2008). Problematically, research has focussed on more direct impacts on native community biodiversity. For example, through increased predation (Crawford et al. 2006; Dick et al. 2012), food competition (Sousa et al. 2008) and disease vectoring (Alderman et al. 1990; Holdich & Reeve 1991) in aquatic environments. Few

studies have assessed geomorphic impacts of invasive species (Fei et al. 2014); with exeptions including bank destabilision from burrowing 'American Signal Crayfish' *Pacifastacus leniusculus* (Dana 1852: Usio & Townsend 2004; Johnson et al. 2011; Harvey et al. 2011) and 'Chinese Mitten Crab' *Eriochier sinensis* (Milne Edwards 1854: Dutton and Conroy (1998) alongside seasonal die-back effects by riparian 'Himalayan Balsam' *Impatiens glandulifera* (Royle: Roblin 1994; Sheppard et al. 2005). As establishment rates of aquatic invasive organisms appear increased across global freshwaters (Strayer 2010); newly arriving taxa could have important geomorphic impacts in rivers and should be subject to investigation (Harvey et al. 2011).

One example of a species with potential to cause geomorphic impacts in rivers is the mollusc *Dreissena rostriformis bugensis* (Andrusov 1897), known as the 'quagga mussel'. A native of the Ponto-Caspian, *D. r. bugensis* has invaded widespread freshwater systems across continental Europe and the North American Great Lakes (Mills et al. 1996; Karatayev et al. 2015). Once established it can form dense, epifaunal colonies on river and lake beds (Mills et al. 1999; Wilson et al. 2006), where agglomerates of live and dead mussel shells increase substrate complexity and surface area (Stewart et al. 1998). Generally, such impacts have been associated with increased density and richness of benthic invertebrates (Stewart and Haynes 1994; Ward and Ricciardi 2007); though *D. r. bugensis* suspension feeding can also reduce phytoplankton communities in the water column (MacIsaac 1996; Horgan and Mills 1997; Hecky et al. 2004). Highly fecund and with robust adult shells, (Czarnołęski et al. 2006; Kobak et al. 2010), mussel individuals attach to the substrate with thread-like byssus to anchor against dislodgement from both flow and predation pressures (Toomey et al. 2002; Kobak 2006; Peyer et al. 2009). Normally associated with marine molluscs, byssus is shared by all *Dreissena* spp. (Ackerman et al. 1994) and may have particular implications for geomorphic agency.

Composed of keratinous protein, byssus is secreted through a ventral shell opening and extends as a series of branching threads, containing adhesive plaques that attach to surrounding bed particles (Peyer 2009). Byssus persists in the environment long after the mussels themselves have died (Burlakova et al. 2000), shows a capacity to resist breakage at forces exceeding 0.5N (Peyer 2009; Kobak) and is more strongly developed in mussels exposed to flowing, rather than still water (Peyer 2009). For *Dreissena* spp., byssus attachments may be made on solid natural substrate of various particle sizes (Mellina & Ramussen 1994; Roberts 1990) but also artificial piping, concrete banking (Roberts 1990; Schloesser & Nalepa 1994) and the shell material of other molluscs (Wainman et al. 1996). Adult mussels can develop up to 200 separate byssus threads for attachment (Clarke 1952; Roberts 1990); which may bind to multiple surrounding bed particles. In streams dominated by pebble or gravel substrate, *D. r. bugensis* may therefore form shell-byssus agglomerates of biogenically interconnected substrate attached to a single mussel body (**Figure 4.1**).

Figure 4.1 *Quagga mussel* agglomerates with shells attached via byssus to substrate of varying sizes. (Lateral view; labels denote shell length (mm)).

It was hypothesised that given byssus-substrate interactions, *D. r. bugensis* may impact geomorphic processes on river beds by two main mechanisms. Firstly, combined byssus-

connected sediments would theoretically require greater hydraulic stress for movement than if particles were unconnected. For example, byssus-sediment agglomeration could simulate increased mean grain size (associated with higher critical shear stress in rivers; Parker 1990; Wilcock 1993) and potentialy mimick compactive stabilisation effects of macrophyte roots (See: Abernethy and Rutherford 2000; Micheli and Kirchner 2002). Secondly, byssus-substrate binding may form more stable mussel shell structures protruding from the substrate bed surface (Peyer 2009); such features been shown to influence near-bed flow dynamics by increasing bed hydraulic roughness (Frostick et al. 2014). In particular, this may cause reduced stream flow velocities nearer the stream bed alongside increased flow turbulence.

No studies to date have examined such dynamics with freshwater epifaunal mussels, though work on comparably sized bivalves (<50mm shell length) from marine environments provides support. For example, flume experiments on live specimens of *Mytilus edulis* (Linnaeus 1758; the 'edible mussel'), utilising byssus attachments, were associated with increased stabilisation of natural bed materials (Widdows et al. 1998; Widdows et al. 2002). For marine epifaunal mussels like *Atrina zelandica*, byssus attachments may also stabilise protruding shell structures on the stream bed; causing reduced near bed (longitudinal) flow velocity and increased flow turbulence (Green et al. 1998; Nikora et al. 2002; Fredrichs et al. 2009). Given precedent in the marine environment, we suggest that in lotic, freshwater systems quagga mussels could (i) increase sediment stability, (ii) reduce near-bed longitudinal flows and (iii) increase near bed flow turbulence.

For this study, *ex-situ* flume experiments were conducted to investigate geomorphic impacts of *D. r. bugensis* within controlled conditions that emulated a gravel stream bed. The first test (experiment 1) aimed to investigate impacts of *D. r. bugensis* on bed stability. Here we examined bedload transport from an artificial test-bed subjected to spate (high velocity) flow conditions and treated with varied densities of *D. r. bugensis* agglomerates worked into the

substrate surface. The second test (experiment 2) investigated impacts of different *D. r. bugensis* densities on near-bed flow dynamics. Here we interrogated near-bed flow velocities and flow turbulence above a similar gravel bed but subjected to reduced flow velocities found under normal conditions within the UK invaded range of *D. r. bugensis*. Together, both experiments were planned to elucidate geomorphic traits of this concerning invasive species and allow discussion on possible implications for cohabiting lotic organisms.

Methodology

Retrieval of test specimens and flume bed substrate.

In September 2017, 120 *D. r. bugensis* agglomerates and ~65kg graded of fluvial gravels were sourced for both flume experiments from the Wraysbury River, UK. This was a short (~8.7km), shallow (< 0.5 m depth), tributary of the river Thames located in a Devensian gravel catchment near Staines-upon-Thames, west London. We chose a downstream sampling site for collecting *D. r. bugensis* agglomerates (Lat -51.451842; Long -0.520814) where the river was approximately 5m wide and characterised by a sandy, gravel/pebble substrate. According to a pilot study, mean *D. r. bugensis* density at this location was 198 individuals m^{-2} (Mills 2017; unpublished data): the highest recorded in the UK at the time. A second, upstream site was used to source fluvial gravels for our flume experiments (Lat -51.459056°; Long -0.517389°; **Figure 4.2**). Here, *D. r. bugensis* had not been recorded and the probability of resident mussels or legacy byssus deposits confounding the gravel's morphological characteristics was considered low.

When sampling *D. r. bugensis* agglomerates at the downstream site, benthic materials were disturbed and collected with pond-net sweeps (1mm mesh size). Bankside inspection of net contents suggested all live *D. r. bugensis* collected had byssus attachments to two or more gravel/pebble clasts (as in **Figure 4.1**). For our experiments we only collected mussel-substrate

agglomerates formed by live, adult *D. r. bugensis* (24 - 36mm shell length) and where byssus attachments were made to certain sized gravel clasts alone (each particle diameter between 8-16mm). This standardisation was chosen so that substrate components of each agglomerate could be matched with the size range of fluvial gravels used for our flume's experimental test bed. In particular, care was taken during inspection and transport of specimens to avert damage to shell and byssus attachments. All mussels selected for the study (n = 120) were killed and preserved inside individual 50ml vials containing Industrially Methylated Spirit (99%). Mean *D. r. bugensis* shell length, number of byssus-attached gravel clasts and total wet weight of agglomerates varied within our selection criteria (See **Table 4.1**; overleaf).

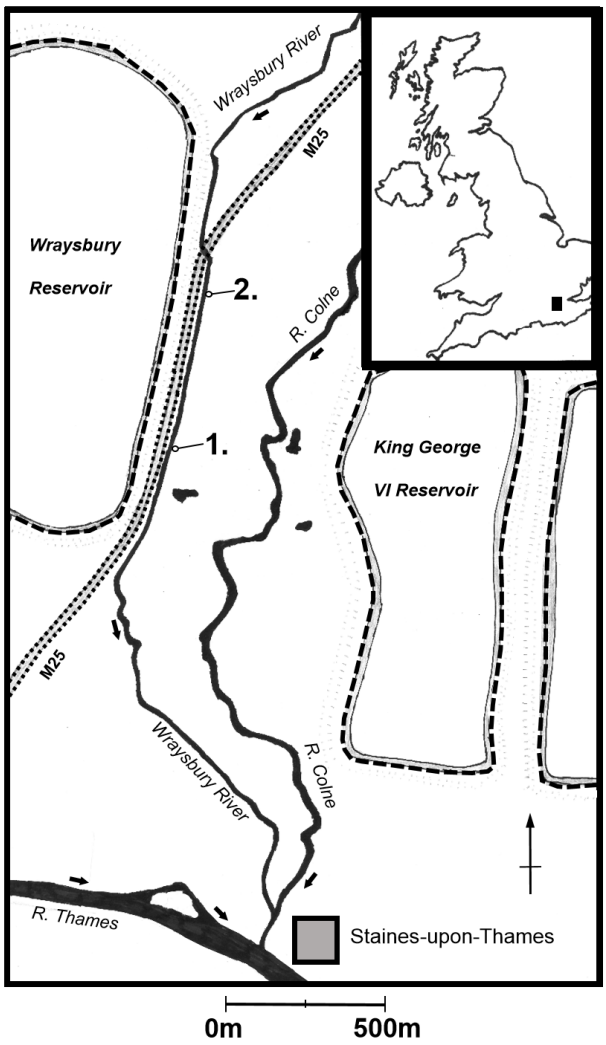


Figure 4.2 Location of the Wraysbury River (~Lat 51°27'08.1"N; 0°31'13.9"W) and sampling sites for (1) *D. r. bugensis* test specimens and (2) fluvial gravels used in experiment.

Table 4.1 Characteristics of tested *D. r. bugensis* mussel-substrate agglomerates (*n* =120) used in both flume experiments.

	Agglomerate weight (g)	No. gravel clasts in agglomerate	*D. r. bugenis* shell length (mm)
Mean ± SE	11.4 ± 0.3	5.3 ± 0.2	28.5 ± 0.2
Median	10.8	5	28
Value Range	5.5 - 24.5	2 - 14	24 - 36.0

We collected fluvial gravels (c. 65g) from the river bed at the upstream site with a spade and used bankside field sieves for grading the clasts at a diameter range of 8-16mm; matching the individual substrate components of collected *D. r. bugensis* agglomerates. All graded gravels were then transported to the laboratory and heated at 200^{o}C for 5 hours prior to use in our experiments. This removed biofilm and detrital organic matter which could confound clast morphological characteristics while also acting as biosecurity precaution. Only gravels from the Wraysbury River were used in the flume set up.

Flume setup

Both experiments were conducted in a tilting laboratory flume with glass walls (channel dimensions: 5m x 1m x 0.5m; see Johnson et al. 2011) using an identical channel set-up. Plywood roughness boards were firstly inserted down the length of the flume, raising the bed by 16cm. In efforts to create naturalistic flow, turbulence artefacts and boundary layer formation during flume runs, top surfaces of each board were treated with a glued layer of fluvial gravels. Here, collected gravel material (from Wraysbury River) was screed onto a 2mm film of tile adhesive and left to dry for 48 hours. A rectangular pit was then cut into the (plywood-raised) bed at the centre of the flume channel, 3.5m down its length (dimensions: 0.5 x 0.4 x 0.16m; long edge oriented streamwise). This was filled with loose fluvial gravels and screed flat at the same height as surrounding roughness boards to create an experimental test bed continuous with surrounding surfaces. For use in experiment 1 a bedload ‘slot’ sampler

was constructed which fitted closely inside a second pit at the most downstream extent of the flume. The sampler was comprised of a steel meshed basket (dimensions = 0.4 x 0.5 x 0.15m) with its lower and side edges wrapped in surber sampler netting (mesh size 1mm). When first running the flume, we used a ruler and Valeport electromagnetic flow meter to undertake a series of *pre-hoc* depth and velocity tests upstream and downstream of the test bed. We found the flow to be uniform and steady throughout the flume channel at moderate pump settings (velocity 0.2-0.3m^{-1} s^{-1}), when mechanically set to a 0.0^{o} elevation.

Experiment 1-sediment transport

This experiment was undertaken under spate flow conditions, exceeding longitudinal stream velocities critical for particle entrainment. The test was designed to measure sediment transport from an artificial, water-worked river bed (herein termed 'test bed') treated with different densities of *D. r. bugensis* agglomerates. Five identical flume runs were conducted for each of two test-bed treatments with 25 or 50 agglomerates, respectively. In both cases, *D. r. bugensis* agglomerates were randomly chosen from those collected at Wraysbury River and placed equidistantly throughout the test-bed surface. To simulate natural observations at Wraysbury River, byssus-substrate components of each agglomerate (see: **Figure 4.1**; 85 pp.) were gently worked into the top surface of the test bed while the mussel shell protruded from the surface, orientated in a randomised direction on the posterior keel (See **Figure 4.3**). Considering the size of the test bed, densities of *D. r. bugensis* per treatement corresponded to 125 and 250 individuals m^{-2}, respectively. For reference, the highest density populations of *D. r. bugensis* found at Wraysbury River had been 130 individuals m^{-2} (Mills et al. 2017; see: **Chapter 2**; 30 pp.). For control treatments, a second set of identical of runs were conducted but where the test bed either contained no *D. r. bugensis* agglomerates, or the same but without water-working (*n*=5 x 2). The latter tests were undertaken for cross-control comparisons demonstrating efficacy of our water-working measures (see: overleaf for details on water-working process).

Water-working of test bed gravels (and *D. r. bugensis* agglomerates where present) for 3 hours was the first phase of each flume run and was undertaken to encourage naturally dynamic armouring of the bed. The channel was filled slowly with water (to limit sediment disturbance) before an increase to the flume pump speed was applied. For water-working, flows were achieved and maintained where shear stress on the test bed was slightly above the point required for particle mobility. Any sediment displaced into the downstream bedload sampler during water-working was reintroduced just upstream of the test bed to allow naturalistic reintegration by flow processes. For each run across *D. r. bugensis* treatments, identical flume pump and tail-weir settings were applied during water-working. In all cases, particle mobility was visually observed to occur during this time. Throughout, flow velocity was recorded every 15 minutes with a Valeport electromagnetic flow meter placed at 0.6 depth 2m upstream of the test bed, using a 1 minute average-reading function.

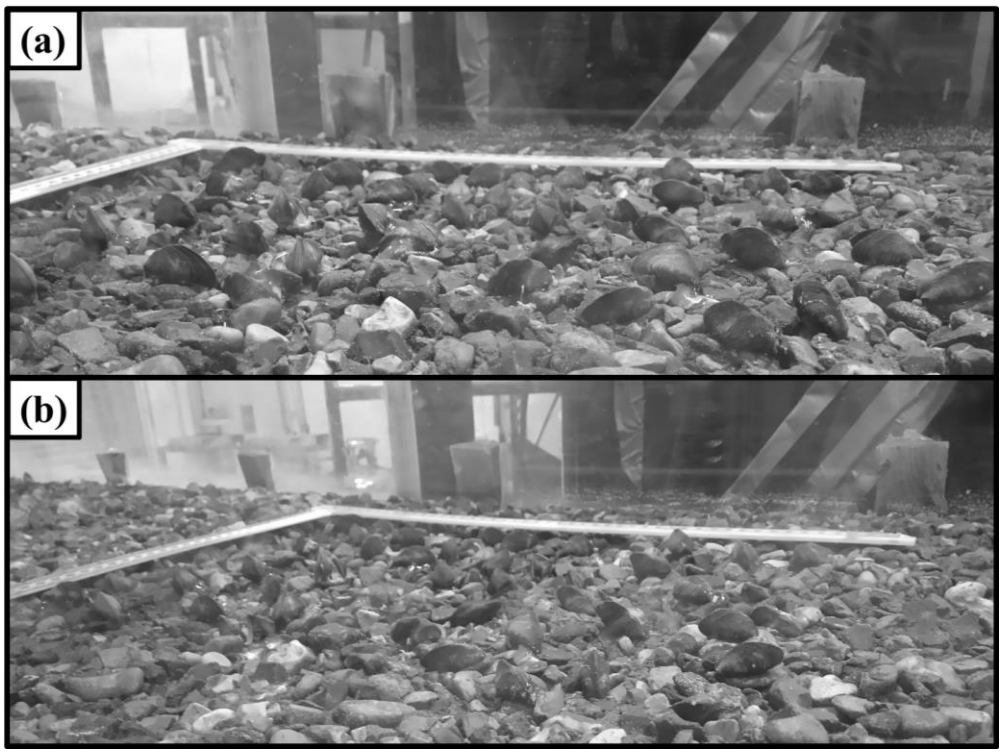


Figure 4.3 *D. r. bugensis* agglomerates worked into the test bed sediment at the start of a flume run (dry conditions). Photograph *a* = 50 *D. r. bugensis* treatment (equivilant to 250 individuals m^{-2}) and *b*= 25 *D. r. bugensis* treatment (equivilant to 125 individuals m^{-2}).

Across each treatment, topographic profiling of the test bed was undertaken for every experiment run both before and after water-working measures. This was undertaken to assess changes to bed topography following waterworking and assess process efficacy. Using a laser profiler (model HRBP-1070, HR Wallingford Ltd) attached on a traverse overhanging the flume (traverse model HRTP-0098, HR Wallingford Ltd.), systematic elevation measures were taken in a streamwise direction across the test bed, along 10 parallel transects. Transects were laterally placed 20mm apart across the width of the test bed with 2D surface elevation recorded every 1mm down their length. Using the inclination index I_l of Smart et al. (2004), we compared the proportion of positively sloping to negatively sloping topographic changes in a streamwise direction down each transect. After water-working, the test-bed substrate was expected to present more asymmetric distribution of inclinations due to increased surface imbrication. Index values tending to a maximum of +1.0 would suggest increasingly structured fluvial substrate, whereas values closer to 0 a more unstructured substrate:

$$I_l = \frac{p_l - n_l}{p_l + n_l + z_l}$$

Where per transect, p_l is the number of positive slopes streamwise, n_l the number of negative slopes and z_l the number of zero slopes.

Following each experimental run's water-working phase we conducted the entrainment phase under spate (high flow velocity) conditions. Here, flume pump speed was increased to an identical level across *D. r. bugensis* treatments and the tail gate was simultaneously lowered by 0.35m so that stream depth (0.28m) was maintained at a consistent level to the water

working phase. Across all treatments, this process achieved flows clearly exceeding that critical for particle entrainment; which were maintained for one hour per run. During this time, bedload and flow velocity measurements were collected every 5 minutes. Bedload measurements were made by emptying the downstream bedload sampler and weighing collected sediment (dry weight) transported from the upstream test bed. In a similar manner to the water-working phase, flow velocity was measured throughout the entrainment phase, i.e. with a Valeport electromagnetic flow meter placed 2m upstream of the test bed at 0.6 depth, using the 1 minute average function. For all experimental runs, calculation of sediment flux (kg m s^{-1}) and total bedload transported (kg m^{-1}) were made from the bedload measurements.

Experiment 2-near-bed river velocity

Our second experiment examined near bed flow dynamics under 'normal' flow conditions analagous to mean stream velocity observations from Wraysbury River, Surrey; within the known *D. r. bugensis* UK range (~0.2m s^{-1}, see: **Chapter 2** and **3**; 30 pp. and 57 pp., respectively). Detailed measurments of flow hydraulic conditions at different depths above the test bed were undertaken across three substrate treatments of either 50, 25 or 0 (control) *D. r. bugensis* agglomerates. For each experimental run, test bed materials, *D. r. bugensis* treatment set up and water-working phases were identical to those for experiment 1. However, in this case, flow-depth profiles were measured using a Vectrino Acoustic Doppler Velocimeter (ADV; Nortek Ltd.) installed on the automated traverse system above the flume (in place of the laser profiler used in experiment 1). This allowed the ADV probe to be precisely lowered into the channel at discrete positions above the test bed to record flow velocity at *x*, *y* and z orientations throughout programmed stream depths. Per *D. r. bugensis* treatment (i.e. 50, 25 and 0 mussels), six replicate flume runs were conducted to provide flow data for the each of three vertical flow velocity profiles. Across all experiments, the velocity profiles were measured from three identical 'profile positions' above the test bed. These were each 0.3m

from the upstream limit of the test bed to a right-hand, central and left-hand (streamwise) orientation: 10cm, 20cm and 10cm from its lateral margins, respectively.

Following the water working phase per experiment run (at identical flume setting to experiment 1); we moderated the flume pump speed to achieve reduced flow rates (0.2- 0.3m s^{-1} at 0.6 depth) but maintained a 28cm stream depth by increasing the flume tailgate height by 20cm relative to the water working phase. Once achieved, flow velocity was measured for each of the 3 vertical profile positions, every centimetre from the stream bed up to 10cm, every 2cm from 10cm to 16cm and every 3cm from 16cm to near the water surface at 25cm. Measurements were concentrated nearer the flume bed to best capture boundary layer conditions most relevant *in-situ* to benthic organisms. At each depth, the ADV was run for 30 seconds at a 20Hz sample frequency, taking approximately 6000 flow measurements x 16 depths per profile.

Analysis

For experiment 1, graphical summaries of sediment flux (kg m s^{-1}) were made using measured means per 5 minute period across *D. r. bugensis* treatments. Mean total bedload transported (kg m^{-1}) per treatment was also graphed and 1-way ANOVA was conducted to assess differences in variation for this parameter between mussel density treatments. For experiment 2, we firstly filtered the raw ADV data using the Vectrino + program (Nortek Ltd.) to eliminate poor signals on a basis of <20% signal to noise ratio and <90% correlation between *x*, *y* and *z* axis measurements. Anomalous spikes were also removed according to the phase-space threshold method of (Goring and Nikora 2002) using the Vectrino + program. Velocity profiles which graphed mean velocity with height from the stream bed were then made for each measurement orientation (*x*, *y* and *z*) and velocity profile position (right, left and centre of test bed) for all treatments. With velocity measurements from each directional orientation of flow (*x*, *y*, and *z*) we calculated a value of Turbulent Kenetic Energy (TKE) to summarise the strength of near-bed velocity fluctuations across treatments. TKE is the product of the flow

variances from the mean during a given period (in our case; 30 second ADV measurements at 20Hz) through vertical (w'), streamwise (u') and cross stream (v') components of velocity (Pope 2006). It may be defined as:

$$\mathrm{TKE} = \tfrac{1}{2}\rho(\overline{u'^2} + \overline{v'^2} + \overline{w'^2})$$

Where ρ is the density of the fluid (1000kg^{-1} m^{-3}).

Following calculation of TKE for all near-bed velocity measurements (0-5cm from the substrate surface) mean TKE profiles per treatment were graphed and a 1-way ANOVA analysis was conducted to assess near bed differences in TKE among the mussel density treatments. Graphing and statistical testing was completed using Sigmaplot v13.0 (Systat Software, Chicago, IL, USA).

Results

In experiment 1 flume hydraulic conditions within water working and entrainment phases were highly consistent across *D. r. bugensis* treatments. Parameters were constrained to a small range of means during water working for stream *x* flow velocity (0.74-0.75m s^{-1}), depth (0.28-0.28m) and discharge (0.13-0.13m^{-3} s^{-1}). Similarly, across spate phases (during entrainment measurements), the range across treatments for mean *x* flow velocity (1.11-1.14m s $^{-1}$), depth (0.28-0.29m) and *Q* discharge (0.19-0.20m^{-3} s^{-1}) was small (**Table 4.2**). This indicated flume hydraulic conditions, including bed shear stress, were highly consistent throughout the experiment and comparison among treatment results would be fair.

Table 4.2 Mean flow parameters per run during water-working (experiment 1 & 2) and entrainment (experiment 1 only) phases across treatments. Longitudinal (*x*) velocity (± standard deviation) was measured using a Valeport flow meter at 0.6 depth $1m^{-1}$, upstream of the test area. Mean flow discharge (*Q* m^{-3} s^{-1}) was calculated by multiplying mean stream velocity (*x*) by the product of stream total depth (*z*) and the flume channel cross width ($0.5m^{-1}$). The term '*n/a*' refers to where water working was not conducted for the respective control treatment.

Treatment	Flume flow conditions	Experiment 1		Experiment 2
		Water-working	Entrainment	Water-working
25 *D. r. bugensis* agglomerates	*x* velocity ($m\ s^{-1}$)	0.745 (±0.01)	1.127 (±0.03)	0.74 (±0.01)
	z total depth (m)	0.28	0.29	0.28
	Q discharge ($m^{-3}\ s^{-1}$)	0.126	0.196	0.124
50 *D. r. bugensis* agglomerates	*x* velocity ($m\ s^{-1}$)	0.752 (±0.01)	1.135 (±0.03)	0.741 (±0.01)
	z total depth (m)	0.28	0.29	0.28
	q discharge ($m^{-3}\ s^{-1}$)	0.126	0.198	0.124
Control (water-worked)	*x* velocity ($m\ s^{-1}$)	0.743 (±0.01)	1.110 (±0.03)	0.741 (±0.01)
	z total depth (m)	0.28	0.29	0.28
	Q discharge ($m^{-3}\ s^{-1}$)	0.126	0.193	0.124
Control (not water-worked)	*x* velocity ($m\ s^{-1}$)	*n/a*	1.143 (±0.03)	*n/a*
	z total depth (m)	*n/a*	0.29	*n/a*
	Q discharge ($m^{-3}\ s^{-1}$)	*n/a*	0.199	*n/a*

Topographic comparisons of the test bed pre and post water working presented varied changes to mean Smart inclination index values (**Table 4.3**). For the control treatments, inclination increased markedly (from 0.007 to 0.038), suggesting higher asymmetry in surface inclinations and greater surface imbrication following water working. The 25 *D. r. bugensis* treatment also presented inclination values that became more asymmetric, but comparably moderately (-0.004 to 0.013). Conversely, inclination values following water working during the 50 *D. r. bugensis* treatments become marginally less asymmetric (from 0.009 to 0.003), albeit with large standard deviation between values **(Table 4.3**). With identical water working methodology across treatments, this case was surprising. Possibly, the higher number of protruding *D. r. bugensis* shells on the test bed surface confounded topographic measurements within the 50 *D. r. bugensis* treatment. Generally, we remained confident in the efficacy of our water working

measures; particularly following comparison of bed load flux across our water worked and non-water worked controls.

Table 4.3 Mean stream-wise inclination index of the test bed across treatments pre and post water-working.

Treatment	Bed condition	Inclination index
25 *D. r. bugensis* agglomerates	*Pre water-working*	-0.0041 ± 0.005
	Post water-working	0.0132 ± 0.008
50 *D. r. bugensis* agglomerates	*Pre water-working*	0.0093 ± 0.008
	Post water-working	0.0030 ± 0.007
Control (water-worked)	*Pre water-working*	0.0065 ± 0.004
	Post water-working	0.0281 ± 0.005

During the spate conditions of the entrainment phase, we observed clear variation in sediment flux and total sediment transported among treatments. The 50 *D. r. bugensis* treatments presented consistely lower mean sediment flux rates compared to the 25 mussel equivilants; which in turn gave lower values than the control tests (**Figure 4.4**). Notably, the non-water worked control presented considerably higher sediment flux rates compared to all other treatments (**Figure 4.4**). Complimenting these observations, mean weight of total bedload transported was lowest for the 50 mussel tests (**Figure 4.5**). Again, the 25 *D. r. bugensis* treatment had lower values lower than both controls and the highest mean total bedload transport was shown for the non-water worked controls (**Figure 4.5**). ANOVAs presented significant differences in mean total bedload transported between treatments. The 50 *D. r. bugensis* treatments had significantly lower mean values compared all others while the 25 *D. r bugensis* treatment was significantly lower than the second, non-water worked control. Finally, the water worked control also presented significantly lower values than the non-water worked control (**Table 4.4**).

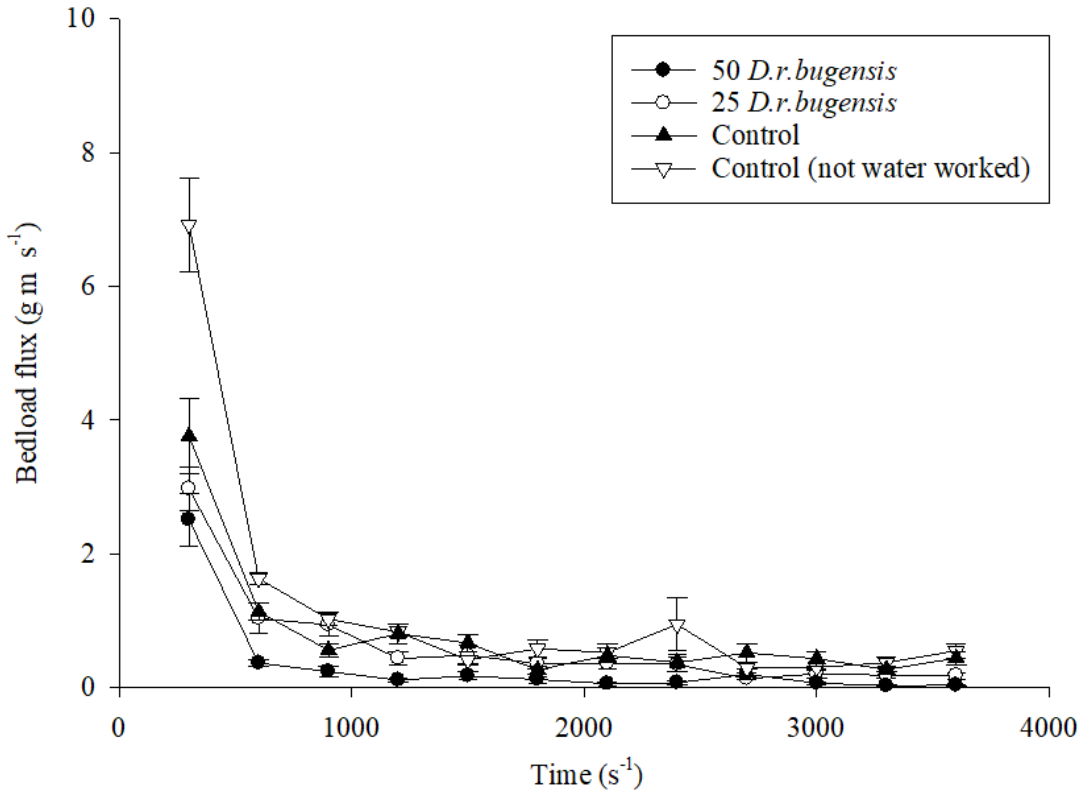


Figure 4.4 Mean bedload flux (g m s^{-1}) during the 60 minute entrainment phase across bed treatments.

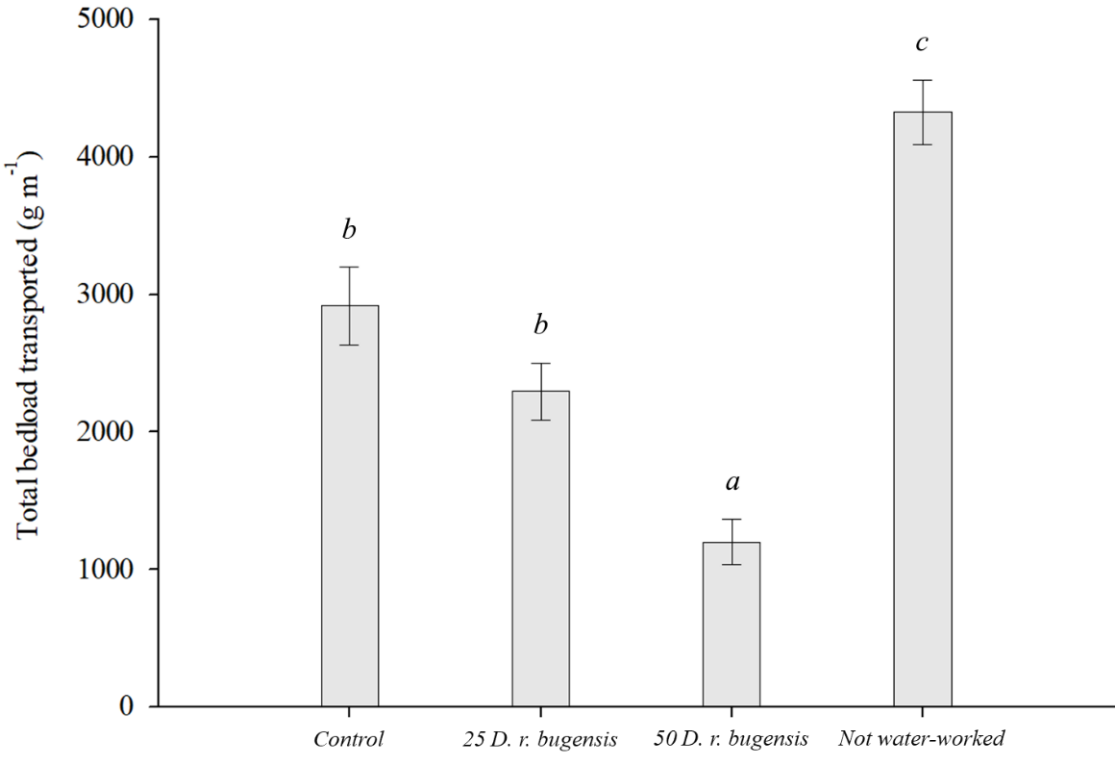


Figure 4.5 Mean total bedload transported during the 60 minute entrainment phase across all bed treatments. Error bars denote standard error. Symbols denote significant differences between test bed treatment categories according to one-way ANOVA and *post hoc* Tukey's test (p = <0.001).

Table 4.4 Mean total transported bedload per test bed *D. r. bugensis* treatment during 1 hour entrainment phase (± SE). Results from ANOVA and Tukey's tests between treatments are also presented.

Test bed treatment	**Bedload Transported** (total as g m^{-2})		**ANOVA** (between treatments)		**Post Hoc Tukey test**
	Mean	SE	Test	*p*- value	
25 *D. r. bugensis*	2296	±208	F(3, 16) = 3	<0.001***	< 0 (not waterworked); > 50
50 *D. r. bugensis*	1202	±162			< all other tests
0 (*Control*)	2917	±282			< 0 (not waterworked; > 50
0 (*not waterworked*)	4324	±233			> all other tests

Experiment 2

In experiment 2, flume hydraulic parameters during water working phases were again, highly consistent among treatments. Values were constrained to a small range of means for stream longitudinal (*x*) flow velocity at 0.6 depth (0.74-0.75m s^{-1}), depth (0.28-0.28m) and discharge (0.13-0.13m^{-3} s^{-1}); similar to values for experiment 1 (**Table 4.2**). This indicated flume hydraulic conditions, including bed shear stress during water working was highly consistent between treatments. In this case, flow parameters were not measured upstream of the test bed during the 'ADV measurement phase' because the Valeport flow meter had to be removed to allow space for the ADV and flume-traverse installation.

During the ADV measurement phases, we observed clear near bed variation in longitudinal (*x*) flow velocity between treatments for 2 out of 3 velocity profile positions. ADV measurements taken 1-3cm from the test bed surface at the 'right' and 'central' profile positions consistently presented lower flows during the 50 *D. r. bugensis* treatment compared to all others (**Figure 4.6a** & **b)**. The 25 *D. r. bugensis* treatment also presented lower flow velocities than the control treatment; however, both tests with mussels presented similar flows to the control at distances

from the test bed above 3cm (**Figure 4.6a** & **b**). In contrast, flows at all depths and across all treatments appeared similar for the left-hand velocity profile (**Figure 4.6c)**.

According to ANOVA, there were consistent significant differences in mean near bed flow velocity among treatments for the right and central profile positions, but not for the left (**Table 4.5**). At the central position, the 50 *D. r. bugensis* treatment had strongly significant, lower values compared to all others when measured at 1, 2 and 3cm from the bed. In addition, the 25 *D. r. bugensis* treatment was significantly lower than the control at 2 and 3cm distant from the bed. At the right-hand position, the 50 *D. r. bugensis* treatment had strongly significant, lower streamwise *x* flow than the control at both 1 and 2cm from the bed. Conversely, no significant differences in near bed *x* velocity were found among treatments for the left-hand profile position; except at 4cm distant from the bed where the control presented higher flows than the 50 *D. r. bugensis* treatment; albeit at relatively weak significance.

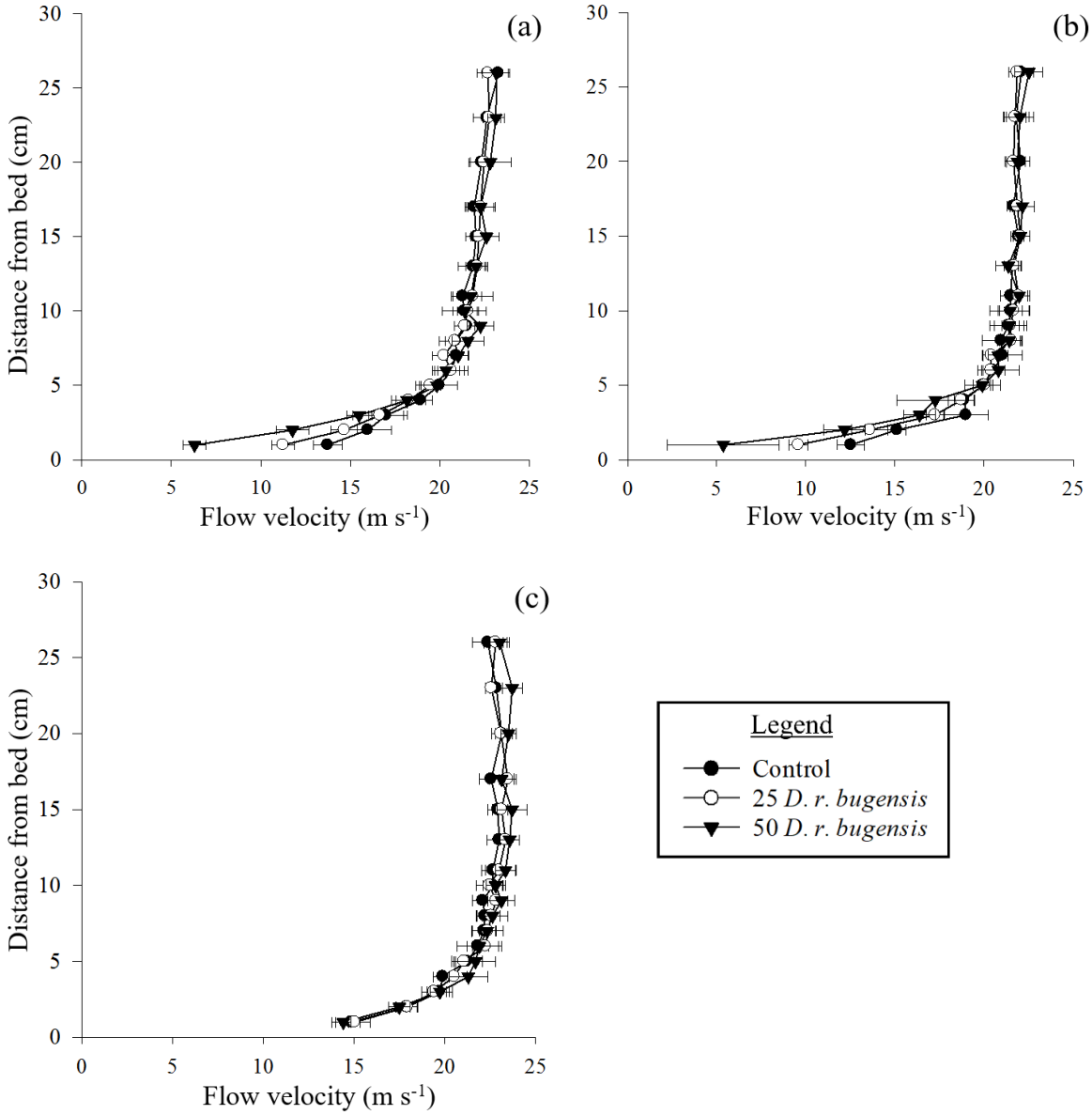


Figure 4.6 Mean longitudinal flow velocity (m s^{-1}) with depth profiles across *D. r. bugensis* shell-substrate agglomerate treatments for the right (a), centre (b) and left (c) of the test bed measured with an Acoustic Doppler Velocimiter (ADV; Nortek Ltd.). At each depth for right, centre and left profiles; 6 experimental runs were completed per treatment and the ADV was run for 30 seconds at a 20Hz sample frequency; taking approximately 6000 flow measurements per run, per depth. Error bars denote standard deviation.

Table 4.5 Mean streamwise x flow rate (m s^{-1}) 1-5cm from the test bed across 6 runs per *D. r. bugensis* treatment (± SD). Each run with a depth profile measured (i) 10cm right, (ii) central and (iii) 10cm left (streamwise) of test bed centre. Results from ANOVAs between treatments for each profile with Tukey test results where significant differences were found.

Position of profile	Distance from bed	Mean *x* flow (m s^{-1}) per treatment (± SD)			ANOVA		Tukey test
		Control	25 *D. r. bugensis*	50 *D. r. bugensis*	Test	*p* - value	
Right	1cm	13.7 ± 0.8	11.2 ± 0.6	6.3 ± 0.6	$F_{(2, 15)} = 176.3$	<0.001***	all treatments different
	2cm	16.0 ± 1.3	14.7 ± 0.7	11.8 ± 0.9	$F_{(2, 15)} = 26.5$	<0.001***	cont > 50 ; 25 > 50
	3cm	17.0 ± 0.9	16.7 ± 1.5	15.5 ± 0.7	$F_{(2, 15)} = 3.03$	0.078	*n/a*
	4cm	18.9 ± 0.8	18.3 ± 0.9	18.2 ± 0.6	$H = 2.85_{(2)}$	0.240	*n/a*
	5cm	20.0 ± 1.0	19.5 ± 0.6	19.8 ± 1.2	$F_{(4, 20)} = 0.45$	0.645	*n/a*
Central	1cm	12.5 ± 0.8	9.6 ± 0.5	5.4 ± 3.1	$H = 13.35_{(2)}$	0.001**	cont > 50
	2cm	15.2 ± 0.5	13.6 ± 1.0	12.2 ± 1.1	$F_{(2, 15)} = 15.0$	<0.001***	all treatments different
	3cm	19.0 ± 1.2	17.2 ± 0.5	16.4 ± 0.9	$F_{(2, 15)} = 12.1$	<0.001***	cont > 50 ; 25 > 50
	4cm	18.9 ± 0.6	18.7 ± 0.7	17.3 ± 2.2	$H = 4.29_{(2)}$	0.117	*n/a*
	5cm	19.9 ± 0.6	20.0 ± 0.3	19.9 ± 1.0	$F_{(2, 15)} = 0.46$	0.955	*n/a*
Left	1cm	14.8 ± 1.1	15.0 ± 0.1	14.4 ± 0.2	$H = 3.83_{(2)}$	0.148	*n/a*
	2cm	17.9 ± 0.6	17.9 ± 0.6	17.5 ± 0.2	$F_{(2, 15)} = 1.0$	0.391	*n/a*
	3cm	19.7 ± 0.7	19.4 ± 0.7	19.7 ± 0.3	$F_{(2, 15)} = 0.48$	0.627	*n/a*
	4cm	19.9 ± 0.5	20.5 ± 0.7	21.3 ± 1.1	$F_{(2, 15)} = 1.0$	0.027*	cont < 50
	5cm	21.2 ± 0.9	21.1 ± 0.6	21.7 ± 1.1	$F_{(2, 15)} = 1.0$	0.448	*n/a*

* P < 0.05; ** P < 0.01; *** P < 0.001

Calculated from our ADV measurements, incorporating longitudingal (*x*), transverse (*y*) and vertical (*z*) flow vectors, we observed moderate near-bed variation in flow Turbulent Kinetic Energy (TKE) between treatments and across all velocity profile positions. Variation of TKE between treatments was less clear than for longitudinal (*x*) flow velocity and consistent differences could be identified only for the right-hand velocity profile. In this case, TKE values 2 to 5cm from the bed were higher for the 50 *D. r. bugensis* treatment compared to all others. Similarly, the 25 *D. r. bugensis* treatment showed higher TKE compared to the control between 2 to 5cm from the bed (**Figure 4.7a)**. Equivilant trends were not clear for the central and left-hand profile positions **(Figures 4.7b & c**); although ANOVAs presented significant differences in mean near-bed TKE between treatments within all velocity profile positions (**Table 4.6**). At

the right-hand position, the 50 *D. r. bugensis* treatment had significantly higher values compared to all others when measured at 2cm from the bed, and at 3cm when compared to the control. At the central position, both the 50 and 25 *D. r. bugensis* treatments presented significantly higher TKE values than the control at 2cm from the bed. At the left-hand profile position, the 25 *D. r. bugensis* treatment presented strongly significant higher values of TKE than all other treatments at 5cm distant from the bed. In addition, the 50 *D. r. bugensis* treatment was higher than the control at 3cm from the bed (**Table 4.6**). In general, *D. r. bugensis* treatments were associated with higher near-bed TKE values compared to the control.

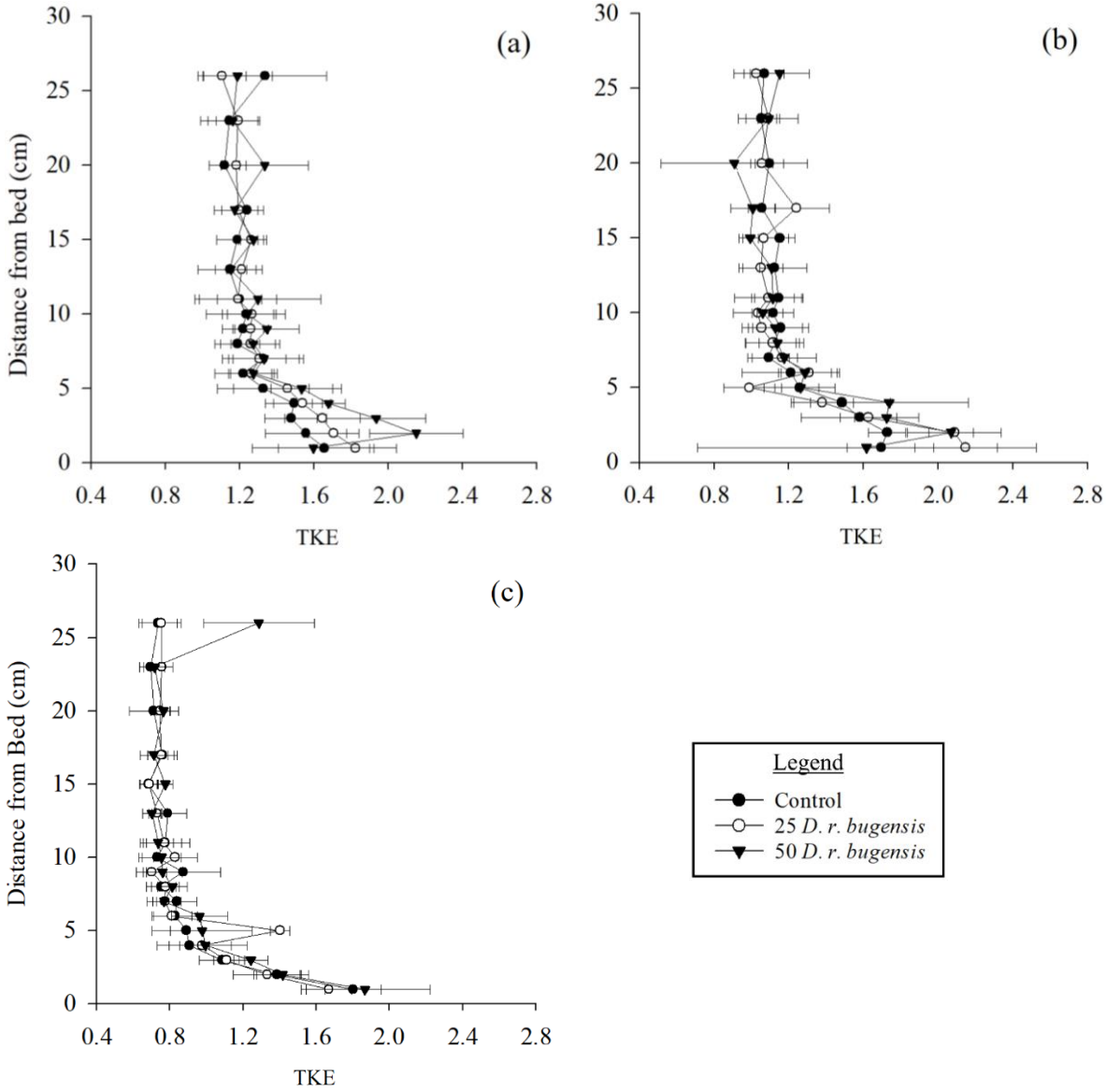


Figure 4.7. Turbulent Kinetic Energy (TKE) with depth profiles per *D. r. bugensis* agglomerate treatment for the right (a), centre (b) and left (c) of the test bed.

Table 4.6 Mean Turbulent Kinetic Energy (TKE) 1-5cm from the test bed across 6 runs per *D. r. bugensis* treatment (± SD). Each run with a depth profile measured (i) 10cm right, (ii) central and (iii) 10cm left (streamwise) of test bed centre. Results from ANOVAs between treatments for each profile with Tukey test results where significant differences were found.

Position of profile	Distance from bed	Mean TKE / run / treatment (± SD)			ANOVA		Tukey test
		Control	25 *D. r. bugensis*	50 *D. r. bugensis*	Test	*p* - value	
Right	1cm	1.66 ± 0.2	1.82 ± 0.2	1.60 ± 0.3	$F_{(2, 15)} = 1.15$	0.344	*n/a*
	2cm	1.56 ± 0.2	1.71 ± 0.1	2.15 ± 0.3	$F_{(2, 15)} = 13.34$	<0.001***	50 > Cont & 25
	3cm	1.48 ± 0.14	1.64 ± 0.20	1.94 ± 0.27	$F_{(2, 15)} = 7.323$	0.006*	50 > Cont
	4cm	1.49 ± 0.15	1.54 ± 0.15	1.68 ± 0.04	$F_{(2, 15)} = 3.098$	0.075	*n/a*
	5cm	1.33 ± 0.25	1.46 ± 0.29	1.53 ± 0.17	$F_{(2, 15)} = 0.925$	0.421	*n/a*
Central	1cm	1.70 ± 0.18	2.15 ± 0.17	1.62 ± 0.91	$H = 4.22_{(2)}$	0.121	*n/a*
	2cm	1.73 ± 0.10	2.09 ± 0.25	2.07 ± 0.12	$F_{(2, 15)} = 8.50$	0.003*	50 & 25 > Cont
	3cm	1.58 ± 0.32	1.63 ± 0.15	1.73 ± 0.17	$F_{(2, 15)} = 0.645$	0.539	*n/a*
	4cm	1.49 ± 0.26	1.38 ± 0.17	1.74 ± 0.42	$H = 4.105_{(2)}$	0.128	*n/a*
	5cm	1.27 ± 0.16	1.05 ± 0.21	1.24 ± 0.09	$F_{(2, 15)} = 3.205$	0.071	*n/a*
Left	1cm	1.80 ± 0.15	1.67 ± 0.12	1.87 ± 0.35	$H = 1.83_{(2)}$	0.402	*n/a*
	2cm	1.39 ± 0.13	1.33 ± 0.19	1.42 ± 0.14	$F_{(2, 15)} = 0.462$	0.639	*n/a*
	3cm	1.09 ± 0.12	1.11 ± 0.07	1.24 ± 0.10	$H = 7.30_{(2)}$	0.026*	50 > Cont
	4cm	0.91 ± 0.11	0.98 ± 0.25	0.99 ± 0.14	$F_{(2, 15)} = 0.462$	0.663	*n/a*
	5cm	0.89 ± 0.09	1.40 ± 0.05	0.98 ± 0.27	$F_{(2, 15)} = 15.98$	<0.001***	25> Cont & 50

* P < 0.05; ** P < 0.01; *** P < 0.001

Discussion

When the test bed was subjected to spate flow conditions, significantly reduced bedload transport was observed for the highest mussel treatment; implying impacts of increased bed stabilization by *D. r. bugensis*. This compliments findings for epifaunal marine bivalve *M. edulis* (Widdows et al. 1998; Widdows et al. 2002) and adds to similar mechanistic impacts shown for *Hydropsyche* spp. caddisfly net constructions (e.g. Statzner et al. 1999; Cardinale et al. 2004; Johnson et al. 2009), riparian plant rooting (e.g. Abernethy and Rutherford 2000; Micheli and Kirchner 2002) and algal biofilm adhesion (e.g. De Brouwer et al. 2005; Vignaga et al. 2013). Futher, with subjection to 'normal' flow conditions, significantly reduced near-bed flows were also observed on the test bed across *D. r. bugensis* treatments in two out of three velocity profiles. This suggests that mussel shells protruding from the substrate could

also provide a bed roughness element; complimenting further work on *M. edulis* (Fredrichs et al. 2009) and similar lotic impacts by the moss *Fissidens regidulus* (Nikora et al. 2003), Canadian pondweed *Elodea canadensis* (Sand-Jensen 1998) and estuarine cordgrass stems of *Spartina anglica* (Widdows et al. 2008). It remained comparably unclear whether alongside flow attenuation, *D. r. bugensis* beds increased stream turbulent kinetic energy, as found for *F. regidulus* (Nikora et al. 2003) and *S. anglica* (Widdows et al. 2008). Nevertheless, for both 'high' and 'normal' flow experiments, our study provided evidence *D. r. bugensis* may act as a geomorphic agent (*sensu* Gutiérrez et al. 2003; Harvey et al. 2011): stabilising bed materials and potentially acting as a surface roughness element. While the author will move to assess clear caveats associated with our experimental design; it is possible that similar trends might occur in natural environments, and potential impacts for cohabiting benthic fauna will first be discussed.

For benthic invertebrates, high flow events can result in significant loss of local abundance and diversity (Scrimgeour and Winterbourn 1987; Cobb et al., 1992). Bed scour from hydraulic shear stress and abrasion from particles in transport may displace individuals into involuntary drift (Bond and Downes; 2003). Those typically scoured from surfaces in high flows (e.g. Imbert and Perry 2000; Gibbins et al. 2009) may benefit if for example, as a roughness element, upstream *D. r. bugensis* attenuated flows below the critical level for dislodgement. Further, Statzner et al., (1984) suggest that for many taxa, involuntary drift only occurs when local bed material itself becomes unstable. In flume experiments, Gibbins et al. (2007) showed 10-fold increases in invertebrate drift occurrence only after consistent bedload transport was observed. With widespread UK taxa either adapted to resist shear stresses at the substrate surface (e.g. of families Elmidae spp., Simuliidae spp., Heptageniidae) or with evasive, burrowing behaviours (eg. of families Ephemeridae spp., Chironomidae spp Unionidae spp.); bed stability may be of particular importance in this regard. Increased bed stability caused by *D. r. bugensis* could

reduce scouring of the substrate during spate events and by effect, the involuntary drift of such taxa.

Further, invertebrates with feeding strategies facilitated by more stable benthic substrate could also benefit from substrate more resistant to transport. Food quantity and availability have been considered important determinants of aquatic community structure (Sweeney & Vannote 1986) and abrasion by saltating sediment in transport has been shown to degrade surficial biofilm; reducing food resources for invertebrate scraper-feeders (Fuller et al. 2010). Such groups could thus also benefit from bed stabilisation by *D. r. bugensis* if it resulted in reduced degradation of biofilm during spates. In the UK, scraper-feeders are widespread and include the majority of freshwater Gastropoda spp., riffle beetles Elmidae spp., mayflies Heptageniidae spp. and caddisflies Glossosomatidae spp. (Mandaville 2002; Thorp & Covich 2009), for example.

Similarly, invertebrates with life histories facilitated by more stable benthic substrate could benefit from geomorphic impacts of cohabiting *D. r. bugensis* beds. Those, for example, which utilise solid substrate for oviposition, including Gastrpods of *Bithyniidia* spp. (e.g. Velecká & Jüttner 2000), and mayflies of Baetidae spp. (e.g. Peckarsky et al. 2000) might experience reduced ovideposit mortality during high flows with a less mobile bed. In addition, more stable surfaces could facilitate the retention of caddisfly structures constructed by various, common UK families. These include feeding nets of *Hydropsychae* spp. (Edington 1968), pupal cases of *Ryacophila* spp., *Hydropsyche* spp. (Statzner et al., 2005) and galleries of Psychomiidae spp. (Alecke et al. 2005). In the case of *Hydrophsyche* spp. net structures, shown themselves to reduce particle mobility (Statzner et al. 1999; Cardinale et al. 2004; Johnson et al. 2009): retention of such features could provide further positive feedbacks to bed stability.

For fish, community composition may also be heavily influenced by substrate stability (Walters et al., 2003; Richardson and Jowett 2002; Jellyman et al., 2013). Common UK lotic taxa such as *Abramis brama* (Linneus 1758; ‘Bream’) and *Rutilus rutilus* (Linnaeus 1758; ‘Roach’) are

associated with relatively unstable river beds in which they upturn and sift substrate material while feeding (Lammens and Hoogenboezem 1991). Alternatively, more selective, scavenging feeders like *Cottus Gobio* (Linnaeus 1758; 'Bullhead') and *Barbatula barbatula* (Linnaeus 1758; 'Stone Loach') have been associated with more stable bed materials where flow refugia and cavities for preferred prey are more abundant (Gosselin et al., 2010; Knaepkens et al., 2002). Cohabiting *D. r. bugensis* might thus facilitate the latter taxa group, better adapted to more stable substrates. The life histories of fish may also be considered, because increased bed stability may provide beneficial protections during juvenile stages. More stable benthic substrates have been associated with increased survival in juvenile populations of goby (Edwards & Cunjak 2007), trout (Erman et al., 1988), char (Shellberg et al., 2010) and salmon (Jensen and Johnson 1999) because during flood events, fewer particles in transport may damage fish by abrasion.

Even during 'normal' flow conditions, influences of *D. r. bugensis* on near-bed hydraulics could also have significant impacts on benthic ecology. For example, variation in stream velocity at the habitat scale has been shown to influence distribution of invertebrates (e.g. Minshall and Minshall 1977; Jowett and Richardson 1989; Growns and Davis 1994), macrophytes and periphyton communities (Dawson et al. 1978; Chambers et al. 1991; Biggs 1996). As a roughness element, the establishment of *D. r. bugensis* beds could firstly attenuate near-bed stream velocities and permit the establishment of ecology associated with relatively lower mean flows. Further, and while not clearly detected in our study, protruding *D. r. bugensis* shells could create near-bed turbulence and microhabitats of flow refugia downstream of shell features (*sensu* Frostick et al. 2014: 134). Studies have suggested the importance of small scale refugia for invertebrate communities (Downes et al. 1993; Lancaster and Hildrew 1993; Negishi et al. 2002) and fish, (Matthews 1986; Pearsons et al. 1992; Gosselin et al., 2010; Knaepkens et al., 2002) while turbulence vortexes may suspend fine sediments (Reidenbach et

al. 2010) encourage nutrient upwelling and oxygen mixing (Tonina and Buffington 2009). Like changes to bedload transport rates, it is clear that alteration to near-bed flows by *D. r. bugensis* could cause varied impacts for lotic ecology.

However, great caution must be taken viewing the experimental limitations of our work. We cannot acknowledge a myriad of possible factors determining *D. r. bugensis* impacts in natural rivers. *Ex-situ* studies in lotic ecology typically simplify or exclude many features of the natural environment (Carpenter 1996; Petersen 1999). Findings may be difficult to directly compare with such systems (Kitchell et al. 1988; Schindler 1998). Firstly, our flume test bed and channel surface was composed and incorporated with only one gravel clast size range. This was not representative of a natural gravel river, where more heterogeneous substrate size classes would be expected alongside associated sorting between fine and coarse particles (e.g. Beschta and Jackson 1979; Petts 1988). In such systems, subtle variation in substrate characteristics may strongly influence bed armouring and mobility (Parker 1990; Gomez 1994; Lisle et al. 2000; Emmet and Wolman 2001). As such, hydraulic properties of bed substrates different to the narrow range tested may override stabilisation or near-bed flow influences of *D. r. bugensis* in some natural rivers. Also, the habitat preferences and potential distribution of *Dreissena* spp. on particular bed substrates has not been investigated in detail. While *D. r. bugensis* have been formally recorded in only one UK river (Aldrige et al. 2014), it remains uncertain whether regionally, mussel densities could commonly reach either treatment scale tested in our study.

Other scales were also highly restricted with our approach. Temporally, we only measured conditions during short periods of specific and steady flow rates. In natural rivers, spates are associated with hydrograph limbs varied in length and intensity; accordant with a myriad of changing environmental conditions (e.g. Hewlett and Bosch 1984; Freer et al. 2002; Lana-Renault 2007). It is possible that the geomorphic impacts of *D. r. bugensis* would be overridden over longer periods with more complex hydrologic regimes present. Further, our experiments

were spatially based solely in a narrow, neutrally elevated flume channel with stable water column depth throughout. Factors such as stream slope, width and depth can be highly influential for particle mobility and near-bed flow conditions (e.g. Shvidchenko and Pender 2000; Walters et al., 2003; Ferguson 2012). Different channel characteristics in some natural environments may override bed stabilisation impacts of *D. r. bugensis*.

Further, like many *ex-situ* studies, our work does not incorporate natural ecological complexity (*sensu* Frost et al. 1998). In particular, *D. r. bugensis* geomorphic agency may be confounded due to other ecological impacts by *D. r. bugensis* where established. For example, in invaded reaches of the North American great lakes, *Dreissena* spp. invasions have been strongly associated with the facilitation of amphipod shrimp species (Stewart and Haynes 1994; Ricciardi et al. 1997); potentially due to increased habitat complexity of mussel beds and provision of refugia from fish predation (Reed et al., 2004; Kobak et al., 2014). Seeing that amphipod shrimps themselves have been associated with bed destabilisation impacts by their foraging activity (Pringle et al. 1993); it is possible mussel-driven amphipod facilitation would counter alternative impacts by *D. r. bugensis*. There remains great uncertainty as to the degree of geomorphic impact *D. r. bugensis* may have in such environments.

To summarize, we must conclude our results only indicate that *D. r. bugensis* has the potential to act as a lotic geomorphic agent. Considering though, clearly important possible impacts for cohabiting ecology, this remains of importance to investigate further. Several options for additional study could be taken to reduce uncertainty surrounding *D. r. bugensis* geomorphic impacts. Firstly, additional flume experiments could replicate our tests with different *D. r. bugensis* densities, substrate grain-size mixtures, hydraulic flow regimes, flume channel dimensions and slope orientations. Such work might also benefit from efforts to increase the naturalism of tested sediments. For example, test-substrates for other flume experiments have been colonised naturally over time *in situ* by a target species before collection and transport to

the laboratory (e.g. Widdows et al. 1998; Johnson et al. 2009). Alternatively, flume researchers have taken casts of natural bed topography for more precise testing of near-bed flow dynamics in the laboratory (e.g. Buffin-Bélanger et al. 2003; Buffin-Bélanger et al. 2006). Such examples could interrogate *D. r. bugensis* impacts in flume conditions which better replicate natural environments compared to this study. Progress in such directions may help elucidate the impacts of *D. r. bugensis* in UK rivers.

Conclusions

1. The invasive Ponto-Caspian mollusc *D. r. bugensis* may be a geomorphic agent where established in rivers. We hypothesised that mussel attachment by byssus secretion to bed substrates may have stabilising impacts on sediment; reducing bedload transport during spate events. Furthermore, we considered protruding mussel shells of *D. r. bugensis*, themselves stabilised by mussel byssus attatchments, could generate increased bed roughness, impacting near-bed flow dynamics during normal flow conditions. Two experiments were undertaken to test these mechanisms of geomorphic agency.

2. In our first flume experiment, graded gravels were subjected to high flow, spate conditions above the critical rate for entrainment. When the gravels were treated with certain densities of *D. r. bugensis* (attached to naturally formed byssus-substrate agglomerates); significantly reduced bedload flux was observed at consistent flow rates, compared to control tests. The largest reduction in bedload transport was found for the high *D. r. bugensis* treatment, followed by the low *D. r. bugensis* treatement; implying an inverse relationship between mussel density and bedload flux.

3. In our second flume experiment, graded gravels were subjected to normal flow conditions below the critical rate of entrainment. In two out of three velocity profiles, gravels treated with certain densities of *D. r. bugensis* presented significantly reduced streamwise velocity between 1-5cm of their surface. Results implied that in some cases *D. r. bugensis* may cause increased

flow attenuation and reduced streamwise flow velocities present at certain densities. In the two profiles where differences were detected, the largest significant reductions in streamwise flow velocity were most consistently found for the high *D. r. bugensis* treatment, followed by the low *D. r. bugensis* treatement. Again, this implied an inverse relationship between mussel density and in this case, near bed streamwise flow velocities. It was comparatively unclear whether *D. r. bugensis* shells caused expected changes to near bed-turbulence.

4. We speculated on some potential impacts of our observations in a UK lotic environment if transferred to a natural setting. For invertebrates, decreased bedload flux cause by *D. r. bugensis* could cause reductions of involuntary drift during spate periods. In addition, increased bed stability may facilitate invertebrate oviposition, scraper-feeding and insect life-history processes. For fish, reduced damage of juvenilles and small taxa by bedload abrasion during high flows could be expected alongside impacts on certain feeding strategies. In terms of changes to near-bed dynamics, we suggested that invertebrate taxa associated with lower stream velocities and flow refugia may be particularly facilitated by *D. r. bugensis* alteration of near-bed hydraulics.

5. Despite clear limitations of *ex-situ* study, it was implied from our results that *D. r. bugensis* could act as a geomorphic agent in lotic environments. Future study might work to confirm this and assess the degree of impact across different environments where invasive *D. r. bugensis* are established. Additional flume experiments could replicate our tests but with different *D. r. bugensis* densities, bed grain-size mixtures, hydraulic flow regimes, flume channel dimensions and slope orientation. Such studies would be strengthened further with the use of more authentic sediment mixtures which potentially incorporate naturally colonised, live *D. r. bugensis*. Progress would help improve knowledge on the impacts of this new invasive species on UK ecology; considered the most potentially threatening in terms of biodiversity (Roy et al. 2014).

Chapter 5: *On ecological impacts of suspension feeding by Dreissena spp. (Bivalva: Dreissenidae) in rivers; incorporating a series of exploratory studies investigating quagga mussel (Dreissena rostriformis bugensis) in the Wraysbury River, UK.*

Summary:

Following establishment of invasive bivalve *Dreissena rostriformis bugensis* in the UK, this chapter aimed to provide a timely discussion of mechansims and potential ecological impacts of suspension feeding by invasive *Dreissena* spp.. With evidence from a series of freshwater environments, the capability of invasive Dreissenid populations to influence organic and mineralogic suspended seston concentrations was underlined; with resultant impacts on cohabiting ecology described for other environments. Particular focus was applied to *Dreissena* spp. feeding dynamics in invaded lotic environments because the known UK range of *D. r. bugensis* was exclusive to rivers at the time of this research.

Notably, literature on the impacts of suspension feeders in rivers was shown to be limited compared to lentic systems; with different impacts apparent across varied hydraulic contexts. Given apparent gaps in knowledge: the results of three exploratory pilot studies, investigating *D. r. bugensis* feeding impacts in Wraysbury River, provide further exploration of how different aspects of fluvial dynamics may influence impacts of *Dreissena* spp. suspension feeding. The first study presented measurements and analysis of an annual survey (2015-16) on stream seston concentrations across the known invaded range. The second study documented efforts to observe change in stream seston concentrations downstream of a particularly high-density *D. r. bugensis* population. The final study presented results of a series of laboratory flume experiments on water from Wraysbury River to assess *D. r. bugensis* filtration rates under controlled conditions.

With reference to these studies and related literature; a simple model was constructed to tentatively estimatate required *D. r. bugensis* densities for clear suspension feeding impacts on stream seston concentrations in the known UK range. Finally, conclusions were arrived at concerning the potential of *D. r. bugensis* suspension feeding impacts on ecology at this site, and other UK freshwaters.

Introduction

Feeding strategies of aquatic invasive fauna impact native biological communities (Ricciardi and MacIssac 2011). Alongside predominantly predacious (e.g. Dick et al. 2002; Crawford et al. 2006; Kreps et al. 2012), herbivorous (Kapuscinski et al. 2012; Moslemi et al. 2012) and detritivorous (Hall et al. 2006; Dumont 2010) taxa; invasive suspension feeders can distinctly influence community structure post-establishment (Malmqvist 2001; Karatayev et al. 2005; Montes et al. 2012). Notably, suspension feeders have been linked to reductions of suspended organic and mineralogic material in lentic (e.g. Holland 1993; Aldridge et al. 2004) lotic (e.g. Roditi et al. 1996; Strayer et al. 1999) and estuarine (e.g. Prins and Smaal 1994; Gerritsen 1994) waters. Materials in suspension, cumulatively termed 'seston,' is considered an important source of energy, carbon and nutrients for ecology in streams and lakes (Whiles and Dodds 2002). Changes to seston availability caused by suspension feeding may influence community structure throughout trophic levels (Strayer et al. 1999; Aldridge et al. 2004).

Invasion of *Dreissena* spp. molluscs to the North American Great Lakes in the late 20th Century generated significant interest in the ecological impact of suspension feeders (Descy et al. 2003; Strayer 2011). The role of *Dreissena* spp. in the advection, circulation and sinking of phytic materials through feeding was considered influential for long term biologic and physicochemical characteristics of invaded systems (Fanslow et al. 1995; Strayer 1999; Vanderploeg et al. 2001). Given the recent arrival of an additonal Dreissenid species to the UK, *Dreissena rostriformis bugenis* (Andrusov 1897), known as the 'quagga mussel' (Aldridge 2014), the aim of this chapter was to compile a timely review of *Dreissena* spp. filter feeding mechanisms and impacts, incorporating discussion on three pilot studies conducted by the author on *D. r. bugensis* in the known UK range.

Like the majority of freshwater mussels (see: Lauritsen 1986; Hakenkamp 1999; Dionisio-Pires et al. 2004), Dreissenids syphon and process stream water to consume suspended phytoplankton such as diatoms, algae, detritus and small zooplankton (see: Madenjian 1995; Horgan and Mills 1997; Dionisio-Pires et al. 2004). Other studies have presented evidence of significant bacterial and blue-green algae components within their diet (Cotner et al. 1995; Vanderploeg et al. 2001); particularly during early larval stages (MacIssac 1992). Research on adult mussels suggested wide variation in the particle size of ingested seston (0.7 to 450 μm^{-1}; Cotner et al. 1995; Sprung and Rose 1988), though within this range, retention rate appeared highest for particles >1 μm^{-1} (Reeders and Bij de Vatte 1990). Efficiency in filtering water for food in suspension is considered high compared to other bivalves (Silverman et al. 1995; Baker et al. 1998); in part enabled by distinct physiological adaptations shared with marine taxa (Ten Winkel and Davids 1982).

For *Dreissena* spp., water is inhaled through a tentacled, ventral-anterior syphon (**Figure 5.1: *a*)** with suspended particles collected in mucocillary currents across the gills (**Figure 5.1: *b***) before ingestion (Morton 1993). At the ctenida, desirable particles are partitioned into marginal food grooves for transport to the labial palps (Baker et al. 2000). Particles on the labial palps (**Figure 5.1: *c*)** then undergo both mechanical and chemical selection (Ten Winkel and Davids 1982; Baker 1998) before ingestion to the mouth (**Figure 5.1: *d***). Overall, particle transport mechanisms within the mussel are similar to those of marine bivalves and the oyster family Ostreidae (Baker 2000) and rejected suspension is cycled and immitted through a second, dorsal-anterior syphon (**Figure 5.1: *e*)**. Discarded particles from the gills are internally transported to accumulate below the ventral-anterior syphon (**Figure 5.1: f)** (Ten Winkel and Davids 1982). Expulsion of discards as pseudofacaes from this normally inhalant syphon occurs by periodic compressions of the shell valves (Morton 1993).

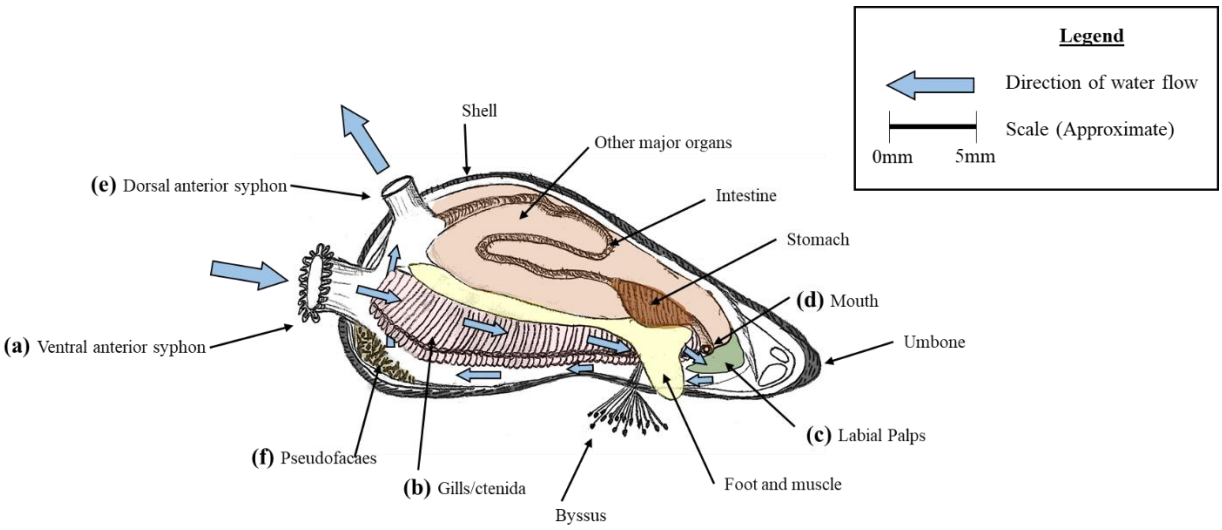


Figure 5.1 Schematic of *Dreissena* spp. filtration and digestive pathway (Adapted from Yonge and Campbell (1968)

Alongside physiological adaptations for suspension feeding, propensity for *Dreissena* spp. to form high density populations has been of significance to their impacts due to the large volume of water whole populations a can filter. For example, abundances of ~16,500 individuals m^{-2} (Lake Michigan; Nalepa et al. 2009), 75, 300 individuals m^{-2} (Lake Huron; Nalepa et al. 1995) and 342, 000 individuals m^{-2} (Lake Erie; Howell et al. 1996) have been recorded in the Great Lakes Region. Given adult individuals have been shown in mesocosm experiments to filter natural water at rates between 114 to 309 ml^{-1} hr^{-1} (Roditi et al. 1996; Diggins 2001); highly abundant *Dreissena* spp. populations may process large proportions of the total water column over short time periods.

Based on laboratory measurements of *Dreissena* spp. clearance of natural seston, it has been estimated natural populations could filter the volume of inner Saginaw Bay, Lake Huron in 1.3 days (Fanslow et al. 1995); the freshwater tidal River Hudson every 1.2-3.6 days (Strayer et al. 1999) and the entire Dutch Ijsselmeer and Markermeer lake systems every 11 to 18 days (Reeders 1989). Given *Dreissena* spp. have been shown to uptake nearly 100% of organic and mineralogic suspended materials >2 μm^{-1} (Jorgensen et al. 1984), the impacts of such feeding

have been readily associated with environmental changes across various freshwaters. In particular, marked reductions in water turbidity have been shown following *Dreissena* spp. invasion of Great Lakes Erie (Howell et al. 1996), Ontario (Barbiero et al. 2006), Michigan (Vanderploeg et al. 2010), Huron (Budd et al. 2001) and Lake St. Clair (Griffiths 1993).

Several ecological feedbacks were associated with such changes. Water turbidity reductions, linked to *Dreissena* spp. seston filtration has been shown to facilitate growth of littoral macrophytes by increasing light penetration (Skubinna et al. 1995; Strayer et al. 1999). Associated removal of algal phytoplankton from the water column may reduce food resources for zooplankton (Maguire and Grey 2006) with negative trophic feedbacks for palaegic, planktivorous fish (Pothoven et al. 2001; McNicke et al. 2006). Correspondingly, *Dreissena* spp. pseudofacaes, containing available nutrients filtered from the water column, may deposit on lake beds; enriching benthic environments for primary production and promoting macrophyte and biofilm growth (Arnot and Vanni 1996; Stoeckmann and Garton 2011). In turn, this can facilitate cohabiting invertebrate communities, providing richer exploitable food resources (Stewart and Haynes 1994; Ward and Ricciardi 2007; Kuhns and Berg 1999). Scraper feeding taxa groups such as Hirudinea, Gastropoda and scavenger-feeding Amphipoda may particularly benefit from resulting increases to primary production (Stewart et al. 1994; Ward and Ricciardi 2007) while dipteran chironomids have been reported to directly feed on mussel pseudofacaes (Griffiths, 1993; Botts et al., 1996). In positive feedbacks to invertebrate facilitation, benthiverous fish such as invasive *Gymnocephalus cernua* 'Eurasian ruffe' may become dominant within fish stocks due to increased prey availability (Herbert et al. 1989).

It is important in caveat that biochemical impacts of *Dreissena* spp. may provide confounding feedbacks to those of suspension feeding. For example, *Dreissena* spp. have been associated with periodic reductions of dissolved oxygen in rivers due to their population respiration demand (Effler and Siegfried 1994; Effler et al. 1996; Caraco et al. 2000). In systems without

adequate reaeration, resulting anoxia may degrade, rather than facilitate benthic fauna (Effler et al. 1996). Alternatively, uptake of calcium by *Dreissena* spp. for shell construction has been associated with reduced whiting events in high alkalinity marl lakes (Barbiero et al. 2005; 2006) and increased light penetration disassociated with phytoplankton clearance. This may facilitate the growth of algal phytoplankton, confounding removals by *Dreissena* spp. feeding (Barbiero et al. 2005). Generally however, *Dreissena* spp. filtering impacts are considered reductive for phytic communities and facilitative for the benthos (Strayer et al. 1999; Ward and Ricciardi 2007).

For aquatic resource managers, general increases to benthic ecological diversity and water clarity can be seen positively; with tentative suggestions for the use of *Dreissena* spp. as biological water quality controls in rivers (e.g. Reeders and De Vatte 1992; Borcherding 2006; Limburg et al. 2010; McLaughlan and Aldridge 2013). This may be problematic, for example because the majority of related research has been undertaken in lentic, rather than lotic environments (Roditi et al. 1996). While, some studies have associated consistent downstream trends of increased water clarity and reduced phytoplankton density with *Dreissena* spp. feeding in the Rivers Hudson (Caraco et al. 1997; Strayer et al. 1999), Oswego (Effler and Siegfried 1998) and Seneca (Effler and Siegried 1994; Effler et al. 2007); research remains poorly repeated compared to lentic environments and typically concerns large, deep river systems in North America. This is of importance because across smaller, higher order streams, typical of many other regions, their impacts may vary for many reasons.

Firstly, Strayer et al. (1999) suggested that for measurable *Dreissena* spp. feeding impacts in rivers, seston must be cleared at rates superseding addition from autochthonous production and allochthonous sources, which might not be possible in certain environments. For example, shallow streams may be exposed to greater sunlight penetration, facilitating photosynthesis and increased algal primary production (Hill et al. 1995; Davies-Colley and Quinn 1998). These

conditions promote algal phytoplanktonic growth which may be high enough to overwhelm removals by suspension feeders. Alternatively, upland streams could be subject to increased run off and associated allochthonous inputs from surrounding catchments due to higher precipitation (Vannote et al. 1980; Correll et al. 2000; Lawler et al. 2006). Additions to suspended seston concentrations may thus be made from materials outside the stream; which again could outweigh filtration removals by suspension feeders. While lentic environments are subject to similar influences, seston fluxes in running waters are likely to be more dynamic. This factor could contribute to confoundment of suspension feeding impacts in rivers.

Regarding stream hydraulics, Dame (2012) asserts the importance of downstream seston advection rates by flow; suggesting observable clearance by suspension feeders would be reduced where hydraulic transport rates of seston are high. Where seston replenishment from upstream is more rapid and particle exposure to resident suspension feeders is short; associated impacts may thus be difficult to detect. Further, Riisgaard et al. (2004) suggest grazing potential of suspension feeders may only be realised with adequate vertical mixing of the water column. The aforementioned lotic studies of Effler et al. (1994, 1996; 1998; 2007) for example, were conducted in slow moving reaches of the Hudson River well mixed by tidal currents. This might not be the case in many, other lowland river environments. Such caveats provide a range of confounding factors for studying suspension feeding *in-situ* and undoubtedly cause variation in susceptibility to impacts across river typologies.

Reflecting these factors, impacts of native suspension feeders on seston in rivers have proved difficult to isolate *in-situ* across various scales. For example, reductions in seston concentrations have been associated with large *Simulium* spp. colonies downstream of lake outlets (Hershey et al. 1996; Malmqvist et al. 2001); but not reliably measured elsewhere for the same taxa. For example, more recent, sophisticated observations on radioactively marked seston in a small Idaho stream (<10m^{-1} width; with comparable *Simulium* spp. populations)

could not detect downstream losses greater than expected by natural sedimentation (Monaghan et al. 2001). In a different approach, Welker and Walz (1998) measured reductions in phytoplankton density down a longitudinal reach of the River Spree, Germany, containing high Unionid and Dreissenid populations. Causation by suspension feeding was deduced by attempts to eliminate other factors of phytoplankton limitation; but not directly proven. Alternatively, Englund (1993) used changes in downstream macroinvertebrate communities to infer suspension feeding impacts of *Hydopsyche* spp. at a Swedish lake outlet. Reduced mayfly recruitment was linked with *Hydropsyche* spp. net capture of early nymph stages (larvae in suspension), while decreased downstream populations of *Simulium* spp. were associated with food competition. In an interesting and unusual study, Morin et al. (1988) applied a selective larvicide to known populations of *Simulium* in a Canadian lake outlet. Seston concentrations were compared in the stream before and after treatment and it was suggested *Simulium* spp. processed between 32 and 55% of total seston flux in the river. This however, according blackfly to population density, corresponded to a clearance rate up to 1000 times higher than expected by estimations from previous literature (Morin et al. 1988). It was possible that other, overriding factors confounded measurements in this case.

A series of three pilot studies, undertaken during this project's wider work, presented factors which could explain such mixed detection success of suspension feeding impacts in lotic environments. In study 1, results of an annual survey (2015-16) of stream seston concentrations across the known *D. r. bugensis* range are presented and analysed. For study 2, a field experiment compared reach-scale seston measurements upstream and downstream of a particularly high-density *D. r. bugensis* population. In study 3, laboratory experiments to measure impacts of *D. r. bugensis* feeding on stream seston were made under controlled, mini-flume conditions. While each pilot study was initially undertaken in an exploratory manner alongside wider project work; by discussing their results, a range of further literature regarding

Dreissena spp. suspension feeding impacts was explored, allowing a tentative assessment on potential feeding impacts of *D. r. bugensis* in UK rivers.

Pilot Study 1 – Investigating *D. r. bugensis* suspension feeding impacts in the Wraysbury River.

The aim of this study was to detect *in-situ* impacts of *D. r. bugensis* suspension feeding down the longitudinal gradient of a river in the known invaded UK range. Between May 2015 and May 2016, monthly observations of stream seston concentrations (DW g^{-1} ml^{-1}) were made at a series of 8 sites on the Wraysbury River, UK. The study reach was 1.8km long and sampling points corresponded to benthic community study sites detailed in **Chapter 2** (30 pp.). We could thus associate observed seston concentrations with concurrent *D. r. bugensis* populations, including for two sites upstream of their known range (sites 1 and 2) and six downstream (sites 3-8; **Figure 5.2**).

As described in **Chapter 2** (30 pp.), the Wraysbury River was the only known lotic environment in the UK invaded by *D. r. bugensis* (Aldridge 2014) and a short (c.8.7km^{-1}) branch of the River Colne, entering the River Thames at Staines, Surrey. Our most downstream sampling site was less than 1.5km^{-1} from this confluence (**Figure 5.2**). The river appeared to have a homogenous stream width (c.5m) and a sandy gravel/pebble substrate throughout. Records collected by the UK Environment Agency between 2015 and 2016, showed mean annual physicochemical conditions of Dissolved Oxygen 10.1 mg L^{-1} ± 0.5 SE, Conductivity 861 µs cm^{-1} ± 12 SE, and Alkalinity 224 mg L^{-1} as CaCO3 ± 7.3 SE (**Appendix IV**; 274 pp). Surrounding land topography was flat, characterised by pastoral moorland and a section of the London orbital motorway.

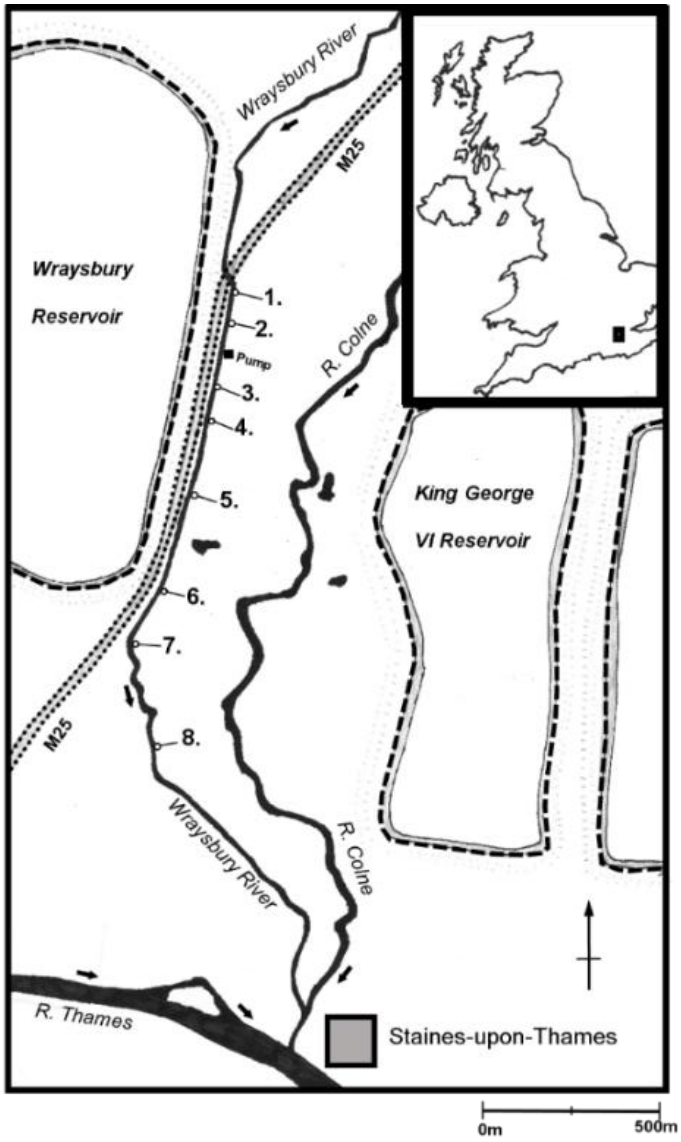


Figure 5.2 Map showing location of sampling site locations for pilot study 1.

Concerning sources of allochthonous materials to the stream: overhanging, deciduous trees were present on the banksides for approximately half the study reach while Heathrow International Airport and the villages of Poyle and West Drayton were located approximately 1km north of site 1, within the wider River Colne basin. Allochthonous inputs to the stream from these sources were expected to be higher during winter months due to increased precipitation rates transporting more materials from the catchment to the river in run-off. As a predominantly shallow stream, (<0.5m depth) the water column was expected to be well mixed with mean annual flow velocity during the study found to as 0.27 m^{-1} s^{-1} ± 0.02 (See: **Table 2.2**; **Chapter 2**; 41 pp.).

Given mean annual *D. r. bugensis* densities of 54 individuals m^{-2} within invaded sites of the study reach (**Table 5.1**); a rough population estimate of 388,800 individuals was made for this section of the river (1.4km^{-1} of 1.8km^{-1}) on the basis of a conservative, 4m^{-1} wide stream bed throughout and simplified as homogenous for indicative purpose. Considering this population estimate, we hypothesised (i.) higher relative concentrations of seston would be found in the upstream sites (1 & 2) compared to the invaded downstream sites (3-8). Also, (ii.) seston concentrations would reduce with increasing distance downstream through the invaded reach. With the latter hypothesis, we thought seston concentrations would particularly decline past the largest *D. r. bugensis* populations at the third and fourth most downstream study sites (See: **Table 5.1**). We finally expected (iii.) stronger reductive downstream trends within the organic matter component of total seston; assuming this would be preferentially assimilated by mussels, rather than exhaled as pseudofacaes.

Table 5.1 *D. r. bugensis* density (individuals m^{-2}) per site and total study reach mean with corresponding Grid References

Site Number	*D. r. bugensis* denisty (m^{-2}) ± SE	*Latitude*	*Longitude*
1	0 ± 0	51°27'37.6"N	0°30'58.9"W
2	0 ± 0	51°27'32.6"N	0°31'02.6"W
3	67.6 ± 8.9	51°27'21.2"N	0°31'08.1"W
4	130.4 ± 18.3	51°27'16.4"N	0°31'09.8"W
5	40.1 ± 8.0	51°27'08.1"N	0°31'13.9"W
6	36.6 ± 5.5	51°26'59.3"N	0°31'20.5"W
7	40.9 ± 5.5	51°26'54.6"N	0°31'25.9"W
8	7.5 ± 1.3	51°26'44.6"N	0°31'23.3"W
Total Mean	53.9 ± 7.9		

Methods

Stream seston concentration measurements were made within the last 3 calendar days of each month, typically the day after macroinvertebrate sampling associated with **Chapter 2** (30 pp.). At each site, we entered the stream in waders, with care to cause minimal disturbance to underfoot bed material. Facing the upstream direction at the centre of the channel, we extended and submersed three replicate 1 L^{-1} polyethylene bottles at approximately 0.5 stream depth. After filling with river water, each bottle was capped, labelled and placed immediately in a cool bag on the bank side for transportation to the laboratory. Sample processing, involving measurement of total seston (g^{-1} L^{-1}) and estimation of seston organic matter (g^{-1} L^{-1}; by loss on ignition (LOI) was completed on return to the laboratory.

In the lab, contents of each bottle were filtered (1 L^{-1} natural stream water) through pre-weighed and pre-dried GF/B fibreglass Whatman filters. Filters with collected materials were then dried in an oven at 50^{o}C for 12 hours (overnight) before reweighing. The difference between pre-filtered and post-filtered weights (g) gave total stream seston concentration (g^{-1} L^{-1}) for three replicates per site, per month. For calculation of loss on ignition (LOI g^{-1}), filters with collected materials were then subjected to 400^{o}C in a laboratory furnace for 5 hours. The difference between initial dry post-filtered weights and 'ashed' post-filtered weights (g) reflected the proportion of seston composed of organic matter (e.g. phytoplankton, bacteria and detritus). To summarise our results, annual mean total and mean LOI of seston per site were graphed by distance downstream the study reach. Similarly, we graphed seasonal mean total and LOI of seston per site based on quarterly means. A series of ANOVAs were then conducted to assess variability of mean total and mean LOI of seston for both annual and seasonal periods. ANOVAs on ranks were used because all data sets remained non-parametric even after logarithmic conversion. Where significant differences were found between sites we conducted

Tukey's tests to determine which differed from another. All analysis was undertaken using Sigmaplot 13.0 (Systat Software, Chicago, Illinois, USA).

Results

Annual mean total seston concentrations appeared relatively stable throughout the study reach within a mean range of 0.005 to 0.007 DW g L^{-1}. There was little difference in mean values between the two upstream sites (outside the known range of *D. r. bugensis*) and those found in invaded reaches. In addition, no gradual reduction of seston concentrations were detected in the downstream direction. Standard error in annual mean seston concentrations was high throughout all sites, indicating strong variation in values found throughout the year (**Figure 5.3**). ANOVAs on rank suggested there were no significant differences of mean annual seston concentrations between any sites throughout the study (**Table 5.2**). Similarly, mean LOI of seston presented little variation across sites with a range of 0.035-0.004 DW g L^{-1} and high standard error. No significant differences were found between sites for annual mean LOI of seston (**Table 5.2**).

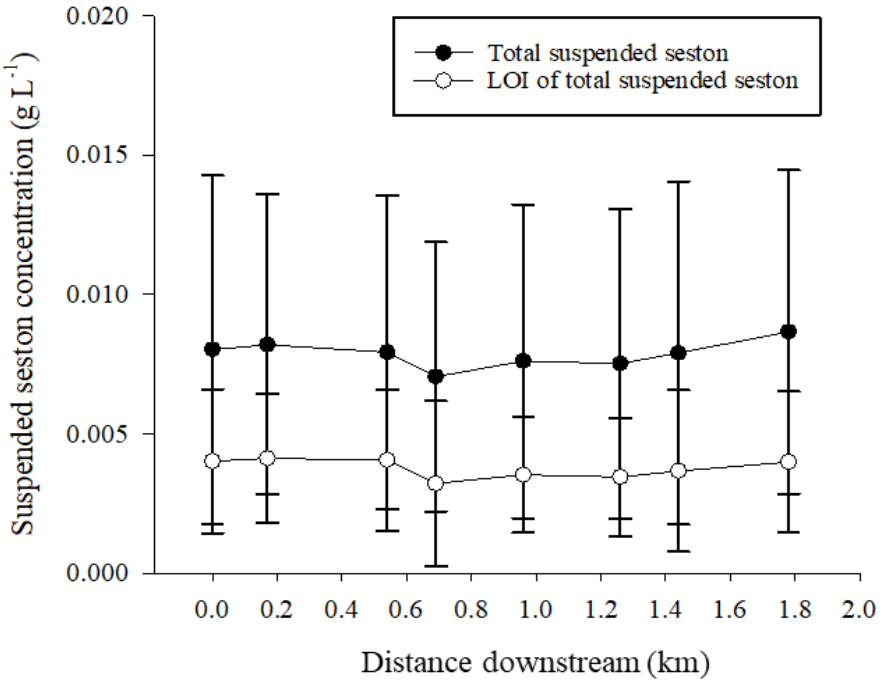


Figure 5.3 Mean annual total suspended seston and seston LOI (g L^{-1}) with distance measured downstream the River Wraysbury study reach (± Standard Deviation).

For seasonal means, winter and spring values for total seston and LOI of seston were both markedly higher than for summer and autumn (**Figure 5.4a & b**). Within seasons, measurements again appeared relatively consistent throughout the study reach, though standard error across seasons was reduced in comparison to annual mean values for both parameters. ANOVAs on rank suggested that there was only one season showing significant difference in mean seston concentrations between sites (Autumn 2015). In this case, site 1 was significantly lower than site 2; both located in a section of the study reach upstream of the known range of *D. r. bugensis*. No significant differences were found between sites for mean LOI of seston within seasons (**Table 5.2**).

Table 5.2 Mean total seston (mg L^{-1}) and Loss on Ignition (LOI mg^{-1}) of total seston in Wraysbury River measured between 2015-16. Results show annual and seasonal means from monthly measurements per site with ANOVA on ranks and Tukey's test results to assess variance between sites. Significant values shown in bold.

Sampling Period	Study Site Number								ANOVA		Tukey's test
	1	2	3	4	5	6	7	8	Test	*p*- value	
(i) *Total seston* (mg^{-1} L^{-1})											
Annual 2015-16	8.03 ± 6.3	8.2 ± 5.4	7.93 ± 5.6	7.05 ± 4.8	7.61 ± 5.6	7.52 ± 5.6	7.90 ± 6.2	8.66 ± 5.8	H = 2.32(7)	0.94	-
Summer 2015	4.11 ± 1.1	3.59 ± 1.9	3.84 ± 2.6	3.54 ± 1.2	3.61 ± 2.5	3.33 ± 2.0	3.18 ± 1.6	3.46 ± 2.8	H = 1.76(7)	0.97	-
Autumn 2015	**2.7 ± 1.6**	5.2 ± 1.4	4.2 ± 2.3	3.6 ± 2.2	3.6 ± 1.3	3.2 ± 1.2	3.5 ± 0.8	2.28 ± 1.2	H = 15.4(7)	0.03*	1 > 2
Winter 2015-16	12.2 ± 7.0	11.6 ± 6.8	10.8 ± 5.5	9.9 ± 5.0	8.7 ± 4.3	10.1 ± 5.4	10.9 ± 6.8	9.51 ± 4.9	H = 2.69(7)	0.91	-
Spring 2016	13.2 ± 4.3	12.5 ± 2.8	13.3 ± 4.4	11.2 ± 4.0	14.6 ± 4.5	11.2 ± 3.5	14.2 ± 3.3	15.7 ± 3.9	H = 9.62(7)	0.211	-
(i) *LOI of Total seston* (mg^{-1})											
Annual 2015-16	4.02 ± 2.6	4.12 ± 2.3	4.16 ± 2.5	3.50 ± 2.2	3.53 ± 2.0	3.45 ± 2.1	3.67 ± 2.9	3.99 ± 2.5	H = 3.44(7)	0.84	-
Summer 2015 (Ln)	2.69 ± 1.0	2.64 ± 1.7	2.12 ± 1.6	2.03 ± 0.1	2.42 ± 2.0	1.93 ± 1.3	2.06 ± 1.1	2.28 ± 2.0	H = 3.09(7)	0.88	-
Autumn 2015	1.83 ± 1.1	2.88 ± 1.3	2.83 ± 1.5	2.29 ± 1.3	1.94 ± 0.9	1.89 ± 1.0	1.92 ± 0.7	2.6 ± 0.7	H = 10.0(7)	0.19	-
Winter 2015-16	5.74 ± 3.0	5.78 ± 2.9	5.52 ± 2.9	4.89 ± 2.5	4.24 ± 1.8	4.71 ± 2.3	5.56 ± 4.49	4.43 ± 2.1	H = 5.94(7)	0.55	-
Spring 2016	5.82 ± 1.8	5.47 ± 0.9	5.89 ± 2.4	4.80 ± 2.2	5.49 ± 1.14	5.33 ± 0.95	5.28 ± 0.7	5.98 ± 2.0	H = 3.88(7)	0.79	-

* P < 0.05; ** P < 0.01; *** P < 0.001

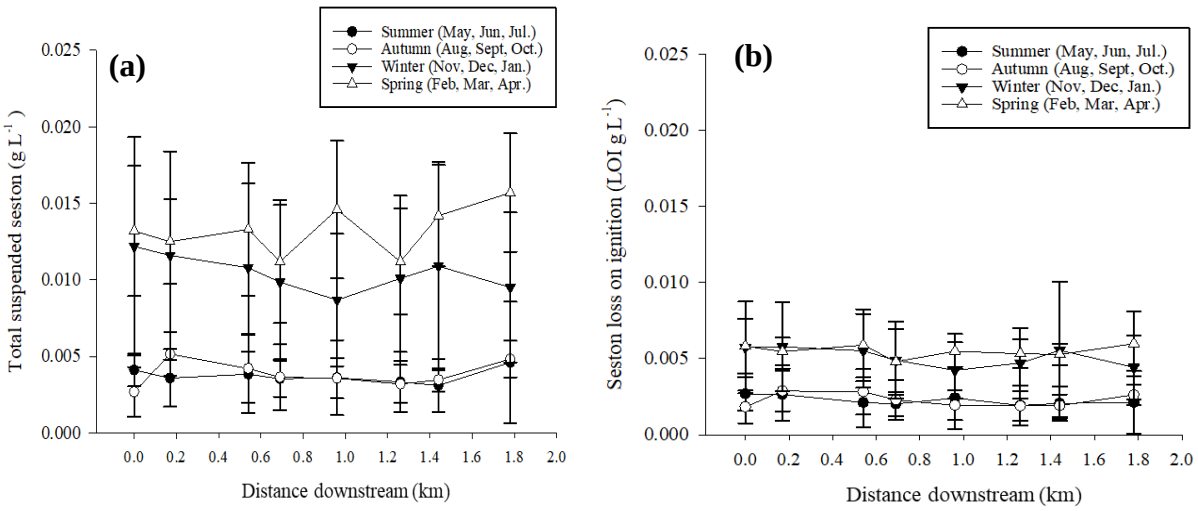


Figure 5.4 Mean seasonal (a) total suspended seston and (b) seston LOI (g L^{-1}) with distance measured downstream the River Wraysbury study reach (± Standard Deviation).

Discussion

Our results implied *D. r. bugensis* suspension feeding did not cause measurable impacts on stream seston concentrations down a longitudinal gradient of Wraysbury River between May 2015 and May 2016. In no cases were significant differences in mean seston concentrations or LOI of seston found between sites, except in one instance for two sites univaded by *D. r. bugensis* in Autumn 2015. There were also no expected reductions of either parameter with increased distance downstream. While this may have been surprising given estimated *D. r. bugensis* populations present; it was considered our null results could have occurred for various reasons.

Firstly, observations showed marked increases to seston concentration in the study reach during winter (Nov, Dec, Jan) and spring (Feb, Mar, Apr) months. Given higher precipitation rates associated with such seasons, it was possible that prior to sampling, increased local run-off caused elevated allochthonous inputs to the stream (e.g. Correll et al. 2000; Lawler et al. 2006). In these cases, seston additions may have overridden filtration impacts from *D. r. bugensis*

(*sensu* Strayer et al. 1999). While alternatively, we neither detected filter feeding impacts during drier summer (May, Jun, Jul) or autumn (Aug, Sept and Oct) months; different confounding factors on seston concentrations may have influenced detection of impacts in these cases. Notably, greater solar exposure and higher water temperatures during summer and autumn (e.g. Hill et al. 1995; Davies-Colley and Quinn 1998) could have increased stream primary production to levels sufficient to override filtration impacts by *D. r. bugensis* (*sensu* Strayer et al. 1999). The high standard deviation of total mean and LOI of seston values throughout our sampling period suggested fluxes of background seston concentrations were significant in the Wraysbury River. However, given the limited resolution of our data, it was not possible to interrogate the cause of these dynamics in more detail.

Future long-term monitoring on feeding impacts by *D. r. bugensis* in Wraysbury River could take advantage of recent advances in data collection technologies. In particular, open source hardware such as the Arduino platfom (see: Lockridge et al. 2016) could provide high resolution, continuous- monitoring, low cost turbidity probes. To date, the majority of potential applications have been unexplored (Langis 2015), but laboratory tests of prototype turbidity loggers have suggested favourable results compared to commercial probes, orders of magnitude more expensive to purchase (See: Kelley et al. 2014). With development of similar, low-cost solutions for monitoring stream height in Costa Rica (Hund et al. 2016), air moisture in Yucatan caves (Beddows and Mallon 2018) and temperature in Spanish agricultural fields (Egea and Pérez-Ruiz 2017); it has been shown field-based durability of low-cost probes is improving (Langis 2015; Lockridge et al. 2016). Their potential for use in monitoring stream turbidity *in situ* could provide greater resolution measurements of seston flux in rivers than previously available. Across annual temporal scales similar to this pilot study; cheap, continuous logging approaches could both elucidate impacts of suspension feeders like *D. r. bugensis* while clarifying the dynamics of confounding, background seston flux in UK rivers.

However, aside from confounding allocthonous and autochonous inputs in the reach; a different, complimentary explanation for our null results was simply that present *D. r. bugensis* densities were insufficient to cause detectable impacts. If mussel densities were low, exposure of stream water to *D. r. bugensis* filtration could have been inadequate for clear reductions of seston down the study reach. Indeed, only two sites (3 & 4) presented mean annual mussel densities higher than 50 individuals m^{-2} (**Table 5.1**). This was significantly lower than recorded for aforementioned studies in the North American Rivers Hudson (2000 individuals m^{-2}; Caraco et al. 1997), Oswego (30, 000 individuals m^{-2}; Effler and Siegfried 1998) and Seneca (61, 000 individuals m^{-2}; Effler and Siegried 1994); where impacts of *Dreissena* spp. suspension feeding were more clearly suggested. While the relatively shallow, reduced stream volume of the Wraysbury River compared to these sites may have somewhat compensated for this factor; we did not make measurements of stream discharge during the study period to assess this. To clarify potential impacts on seston by suspension feeding; future lotic studies should clearly acknowledge stream volume and discharge rates in context to present populations. This conclusion, in particular, guided the design of our second pilot study investigating impacts of *D. r. bugensis* feeding in the Wraysbury River.

Pilot study 2 - Investigating reach-scale suspension feeding impacts downstream of a high-density *D. r. bugensis* population in Wraysbury River.

During completion of our 2017 artificial substrate experiments (See: **Chapter 3**, 57 pp.), it was noted *D. r. bugenesis* densities in some sections of Wraysbury River had increased significantly since 2015-16. Notably, a particularly high density population had become established in an approximately 100m long reach, downstream of study site 5 (Lat 51.451842; Long -0.520814; 198 individuals m^{-2}). Given this, we aimed to detect impacts of *D. r. bugensis* feeding at this

location by comparing stream turbidity upstream and downstream the population within this reach. Our approach followed aforementioned lotic studies of Hershey et al. (1996) and Malmqvist et al. (2001), where suspension feeding impacts of *Simulium* spp. were inferred by clear seston depletion upstream to downstream across a high density population. While our pilot study was undertaken with poor replication in comparison; it was hoped this approach could do better than pilot study 1 at isolating impacts of *D. r. bugensis* suspension feeding in the UK invaded range. In design, particular account was taken of confounding factors to suspension feeding such as allochthonous inputs, primary production, stream water volume and discharge rates.

Stream turbidity (NTU) measurements were compared between an upstream sampling point (Lat 51.451743; Long: -0.520911; **Figure 5.5**) and one 60m downstream (Lat 51.45102; Long: -0.521337) of the high *D. r. bugensis* population identified. Turbidity has been shown in other freshwaters to closely correlate with suspended seston load and in particular, phytoplankton density (Gippel 1995). For example, marked NTU reductions have been associated with filtration by *Dreissena* spp. in various lentic (e.g. Howell et al. 1996; Vanderploeg et al. 2010) and lotic (e.g. Effler and Siegried 1994; Caraco et al. 1997) environments. Given stream densities of *D. r. bugensis* appeared particularly high within our study reach, we hypothesised mean stream turbidity (NTU) would be consistently, significantly lower at the downstream measurement point than that upstream.

Our study was completed between 11th June and 17th July 2018 during a period of continuously dry and fine weather conditions. Given this, we had reason to believe allochthonous input within the reach would be relatively low at this time. In addition, the study site appeared shaded by overhanging vegetation (**Figure 5.5**), suggesting primary production inputs to stream seston could be limited (e.g. Hill et al. 1995; Davies-Colley and Quinn 1998). We anticipated that with low-cost, portable turbidity meters; repeated NTU measurements would provide adequate

profiling of stream seston to compare concentrations between the upstream and downstream sampling points. While we used commercially available, Palintest turbimeters (PTH092) for manual NTU measurements in this case; the study was designed as a proof-of-concept test for future research with Arduino (Arduino AG Ltd.) turbidity loggers in development for long-term deployment at this field site.

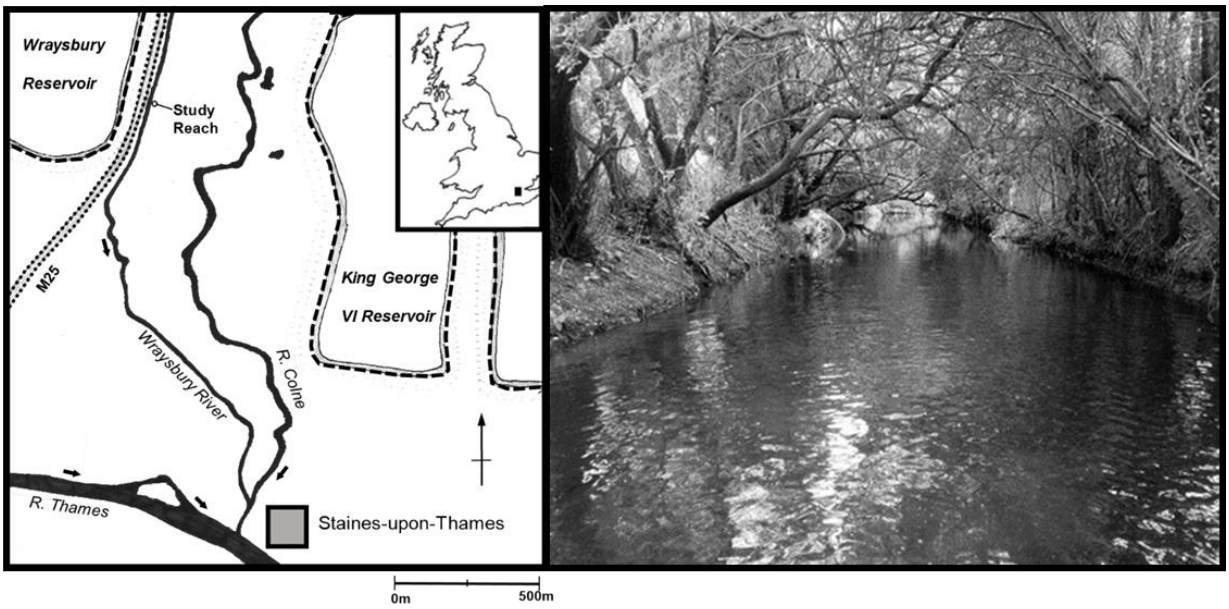


Figure 5.5 Location of study reach (left) and photograph (right) looking downstream from the upstream turbidity sampling point (Lat 51.45174; Long -0.52091) for pilot study 2.

Methods

Before starting our turbidity monitoring, we assessed a series of morphologic and environmental conditions through the study reach on the 11th June 2018. Stream wetted width (m), depth (m) and longitudinal velocity (m^{-1} s^{-1}) were taken in a series of spot samples every 10m streamwise down the reach for $60m^{-1}$ longitudinal distance. Wetted width (m) was measured using a tape extended cross-channel while depth was recorded at $1/3^{rd}$ channel

intervals at the left, centre and right of the channel cross section. Velocity (m^{-1} s^{-1}) was measured at the centre of the channel with a Valeport flow meter using the 30 second average reading. Total mean values of each parameter were used to estimate water volume in the study reach, alongside discharge rates (m^{-3} s^{-1}). Stream temperature was also measured at each sample point using a Hannah HI-98311 temperature probe. To indicate stream solar exposure, light intensity (LUX) was measured with identical spot samples using a SODIAL LX1330B light meter. LUX value comparisons to a series of 10 similar measurements from a nearby section of open bankside were used to approximate solar exposure of the reach. Records collected by the UK Environment Agency in the three months prior to the experiments showed mean values of Dissolved Oxygen 10.0 mg L^{-1} ± 0.6 SE, Conductivity 902 µs cm^{-1} ± 66.3 SE, and Alkalinity 220 mg L^{-1} as CaCO3 ± 66.3 SE (**Appendix IV**; 274 pp.).

A series of 7 daily monitoring experiments were then undertaken using identical methodology throughout. Firstly, a series of 5 drogues were dropped into the centre of the stream at the upstream sampling point. The mean time (s^{-1}) it took for their conveyance by flow to the downstream sampling point provided a rough transport time for particles in suspension down the study reach. This value was used as the time interval (s^{-1}) between coordinated water sampling at the upstream and then downstream points. In both cases, this was undertaken every 5 minutes for a period of 1 hour each day.

Water was sampled from the centre of the stream channel by extending a telescopic sampler from the bank. At least $10ml^{-1}$ of stream water per sample was poured into in a labelled polyethene bag and placed in a cooler box on the bankside. After the 1 hour sample collection period, samples were decanted into discrete $10ml^{-1}$ meter vials and shaken rigorously before analysis using a hand held Palintest turbimeter plus (PTH092). NTU values were recorded for each sample at both upstream and downstream sampling points. Every 5 minute sample during the collection period was considered a replicate for an upstream and downstream mean value

per daily experiment. Following our field visit, on June 17th, mean *D. r. bugensis* density (individuals m^{-2}) was measured in the reach using a 0.33x0.33m^{-1} benthic surber sampler placed at the centre of the channel. Every 5m down the length of the reach, benthic materials were collected to approximately 2cm substrate depth per sample and sorted on the bankside for enumeration of present *D. r. bugensis*.

Analysis

Mean turbidity (NTU) was graphed for upstream and downstream sampling points for each daily experiment (±SE). Within each, we then conducted a series of independent t tests to assess significant variance between mean upstream and downstream turbidity (NTU). Analysis was undertaken using Sigmaplot 13.0 (Systat Software, Chicago, Illinois, USA).

Results

Initial investigations presented a small range of morphological differences throughout the study reach, including for stream wetted width (5.2-5.5m) and depth 33-59cm). The range of streamwise flow appeared similarly homogenous (0.18-0.23m s^{-1}) and means for all parameters were found with low standard error (**Table 5.3**). Using these values, stream discharge was estimated as 0.44 m^{-3} s^{-1} in the study reach. Given a similar range of mean flow rates measured after turbidity measurements on each day of experiment (0.2 – 0.21m s^{-1}); we expected stream discharge to be approximately analogous throughout the study.

Densities of *D. r. bugensis* (individuals m^{-2}), measured immediately after our final turbidity experiment, were found to be higher than previously recorded in the reach. The range found across samples was 165 – 753 individuals m^{-2} with a mean value of 376 individuals m^{-2} (± 90 SE). The range of light intensity within the channel (52-224 LUX) was significantly lower than when measured in the open, outside the channel (1160 – 1217 LUX). Considering consistently

clear weather conditions throughout the study, similar levels of light intensity within the reach were expected across week investigations. Mean stream temperature was 18.3^{o}C ± 0.05SE.

Table 5.3 Summary of study reach physicochemical and *D. r. bugensis* density (individuals m^{-1}) measurements with range and mean (±SE) values from point samples taken at 10m longitudinal intervals.

Parameter Measured	**Range** *all point samples*	**Mean ± SE** *all point samples*
Stream wetted width (m^{-1})	5.2 - 5.5	5.3 ± 0.04
Stream depth (cm^{-1})	33 - 59	41.6 ± 1.2
x Flow rate (m s^{-1})	0.18 - 0.23	0.20 ± 0.01
Estimated Stream discharge (m^{-3} s^{-1})	0.37 - 0.63	0.44 ± 0.03
Water temperature (^{o}C)	18.2 - 18.5	18.3 ± 0.05
Midday light intensity in channel (LUX)	52 - 224	109 ± 23
Midday light intensity on open bankside (LUX)	1160 - 1217	1187 ± 5.4
***D. r. bugensis* density (individuals m^{-2})**	165 - 753	376 ± 90

Across measurements, mean NTU values appeared similar at both upstream and downstream measurement points with moderate standard deviation in each case. NTU appeared to (i) slightly decline down the reach with the 13th and 14th June experiments, (ii) increase with the 11th, 12th and 16th experiments and (iii) was stable for all others (**Figure 5.6**). Mean NTU values across experiments ranged between 7-9 NTU at both sampling points, except for the 14th June experiment, where NTU appeared higher at both points (12-13NTU). Within experiments, tests on variance of mean NTU between upstream and downstream values found no significant differences. Corresponding *p* – values ranged between 1.20 and 0.97 (**Table 5.4**).

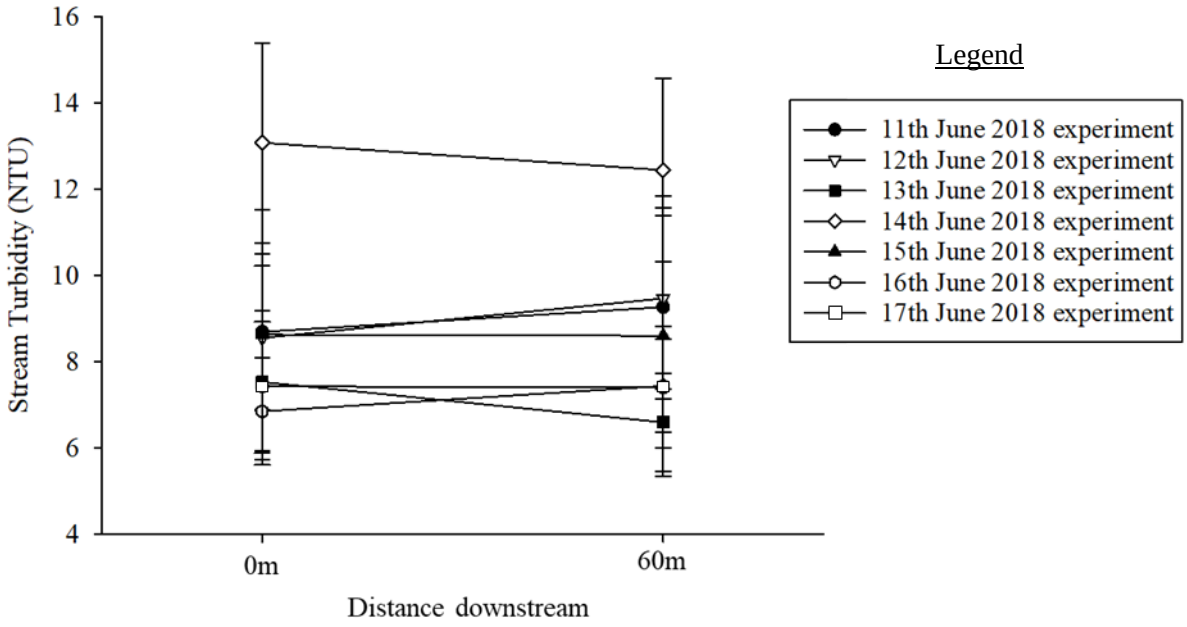


Figure 5.6 Mean stream turbidity (NTU; ±SD) at the upstream and downstream sampling points per experiment.

Table 5.4 Mean stream turbidity (NTU) recorded at the upstream and downstream measurement sites per experiment date on the Wraysbury River (± SE). Results from t-tests and Mann-Whitney Rank Sum tests where data non-parametric despite Log transformations.

Experiment Date	**Stream Turbidity (NTU)**		**t-test**	
	Upstream	Downstream	Test	*p*- value
11th June 2018	8.7 ± 0.53	9.3 ± 0.61	U = 59	0.470
12th June 2018	8.6 ± 0.48	9.5 ± 0.61	U = 66	0.729
13th June 2018	7.5 ± 0.48	6.6 ± 0.33	t = 1.6	0.120
14th June 2018	13.1 ± 0.67	12.4 ± 0.61	U = 48	0.175
15th June 2018	8.6 ± 0.84	8.6 ± 0.94	t = 0.02	0.492
16th June 2018	6.9 ± 0.36	7.4 ± 0.31	t = 0.23	0.229
17th June 2018	7.4 ± 0.43	7.4 ± 0.41	t = 0.04	0.970

* P < 0.05; ** P < 0.01; *** P < 0.001

Discussion

The aim of this study was to detect suspension feeding impacts of a particularly high-density *D. r. bugensis* population on river seston concentrations in the UK invaded range. With no significant decline in stream NTU values from upstream to downstream, expected indications of reduced seston concentrations were not found downstream of the study reach. To some degree, this was surprising. Firstly, it was assumed dry weather throughout the work would mean confounding allochthonous inputs within the reach were limited during our observations. In addition, sunlight exposure appeared relatively low, implying autochthonous algal additions would be subdued. While it was considered, as outlined in **Chapter 4** (82 pp.), other fish or invertebrates could have caused confounding bioturbation effects within the reach (e. g. Hassan et al. 2008; Johnson et al. 2011; Pledger et al. 2016); there was no evidence of taxa present thought to cause such impacts (e.g. crayfish, carp, bream). Further, *D. r. bugensis* was found in the reach at higher mean densities than anticipated at 376 individuals m^{-2}; corresponding to the highest yet recorded in the UK (Pers. Comms. 2018; UK Environment Agency). These factors would have increased the likelihood of observable downstream reductions in NTU values caused by *D. r. bugensis* suspension feeding.

However, with particular reference to our stream discharge estimations, we calculated the most likely reason for our null results was that again that *D. r. bugensis* densities were insufficient to cause measurable impacts at the scale of our reach. Where *Dreissena* spp. individuals have been shown across the literature to filter water at mean rates between 114 – 309 ml hr^{-1} (Roditi et al. 1996; Diggins 2001), the densities required to cause significant reduction in seston concentrations over a small, 60m long reach would probably be much higher than observed in this study. For example, our estimation of stream discharge ($0.44m^{-3}\ s^{-1}$) corresponded to 440 $L^{-1}\ s^{-1}$. Using this value, a simple model was constructed (given the context of a steady flow

rate of $0.2m^{-1}\,s^{-1}$) to estimate the minimum number of *D. r. bugensis* required to filter the whole water volume in transit through our reach.

$$(Q) \div (fl) \div (y) \div (x) \times 0.44 = Min\text{D.b.}$$

Equation 1.

Where:

Q = stream discharge ($0.44\ m^{-3}\,s^{-1}$); fl = the maximum volume of water an individual *D. r. bugensis* may filter in one second ($0.000000086\ m^{-3}\,s^{-1}$; converted from $0.309L^{-1}\,hr^{-1}$ given by Diggins 2001); y = channel width ($5.3\ m^{-1}$); x = channel length ($60m^{-1}$) and Min *D.b.* = the minimum density of *D. r. bugensis* (individuals m^{-2}) required to filter the entire stream water volume.

Using equation 1, we estimated a minimum mean density of 7, 093 *D. r. bugensis* individuals m^{-2} over 60 m^{-1} would be required to filter 100% of the water volume in transit through our study reach; with densities of 709 and 1418 individuals m^{-2} required to filter 10 and 20%, respectively. This was of importance because for the latter cases alone, required mussel densities for 10 to 20% filtration would be 2 - 4 times the mean value found in our study reach. While the respective 376 individuals m^{-2} would theoretically correspond to a 5% filtration of the total water volume; such changes could have been too small to be picked up by instrument resolution. Further, important additional caveats were identified which could prevent such observations.

Commenting on previous estimations of filtration capacity for suspension feeders: Yu and Culver (2001) asserted impacts of re-filtration due to low water column mixing is regularly

overlooked. For example, where the water column is stratified, suspended seston near the surface could pass unexposed to *D. r. bugensis* filtration. Alternatively, seston suspended nearer the bed would be more heavily consumed, where reduction in concentrations could be most evident. This is of importance, because in our study, we assumed a well-mixed water column and sampled from the top of the water column, which may be less exposed to mussel feeding. As such, we may have failed to test the near bed zone of the stream most impacted by suspension feeding. Future development of this study methodology should make efforts to assess the level of stream mixing within the water column to account for this factor.

Further, our use of turbidity (NTU) as a proxy measure for seston concentrations could be problematic due to hydraulic entrainment of fine materials within the $60m^{-1}$ reach. For example, if downstream silt availability was higher compared to upstream sections, mineralogic additions to suspended load could occur (Ellis 1935; Extence et al. 2011). Unless accounted for, this could confound turbidity reductions by *D. r. bugensis* within the reach. For example, when studying *D. polymorpha* feeding impacts in the French River Moselle, Descey et al (2003) predicted that despite reduction of phytoplankton stocks, turbidity in lowland sections would remain stable due to high mineralogic suspension rates. It follows that aforementioned facilitation of macrophyte and biofilm growth by *Dreissena* spp. (due to increased solar penetration) would be limited in such cases; alongside corresponding secondary benefits for certain benthic invertebrates (e.g. scraper and herbivorous taxa).

While our study reach (characterised by gravel and pebble substrate) did not appear to present significant sources of fine materials for suspension; future work *in situ* should ensure more detailed assessment of silt availability to account for this factor. In rivers where mineralogic suspension rates might be high, organic components of seston could be specifically tested, rather than broad NTU measures. In this respect, measurement of chlorophyll-*a* concentrations (mg^{-1} L^{-3}), as a proxy for phytoplankton biomass, has been widely used for analysis of

Dreissena spp. suspension feeding in the Great Lakes region (e.g. MacIsaac et al. 1992; Fahnenstiel 1995; Roditi et a. 1996).

Investigations may also benefit from contextually specific knowledge of *D. r. bugensis* filtration rates, particularly when calculating filtration capacity estimates for known mussel populations. For example, equation 1 assumed constant feeding activity per *D. r. bugensis* individual at the highest mean filtration rates recorded for *Dreissena* spp. in the literature. Several cases have demonstrated variance in mussel feeding activity over time (e.g. Sprung et al. 1988; Fanslow et al. 1995; Horgan and Mills 1997) with mean values for individuals regularly recorded closer to 0.1 L^{-1} hr^{-1}, rather than 0.309 L^{-1} hr^{-1} (e.g. Fanslow et al. 1995; Roditi et al. 1996). In this respect, various factors may influence *Dreissena* spp. filtration capacity. Feeding rates have been negatively correlated to the ratio of mineralogic to organic seston concentrations (Sprung and Rose 1988), again related to contribution from fine, bed substrate components. Also, water temperature may impact metabolic activity (Mills et al. 1996; Descy et al. 2003), with optimal feeding rates shown to occur at 24^{o}C (Aldridge et al. 1995); markedly higher than recorded in our study (mean: 18.3^{o}C). Further, stream flow may be influential, shown to be be inhibitory for suspension feeding at velocities of 0.2m^{-1} s^{-1} and above (Ackerman 1999). Conditions observed in our study reach appeared similar to this level (approx.. 0.2m^{-1} s^{-1}), suggesting *D. r. bugensis* filtering rates could have been sub-optimal at the time of our study.

Overall, this second pilot study failed to present expected evidence for seston reductions downstream of a particularly high density *D. r. bugensis* population in the known UK range. Clear ecological impacts from *Dreissena* spp. feeding activity would thus appear unlikely at the tested scale and current mussel densities. However, several methodological uncertainties were underlined for this study, demonstrating complexity in suspension feeding impact dynamics in lotic environments. Confounding factors such as the degree of water mixing,

resuspended sediment within reach and variable mussel feeding rates could have resulted in failure to detect expected impacts. To help clarify one point of contention, we decided to undertake a final, third pilot study, elucidating potential filtration capacities of *D. r. bugensis* in the Wraysbury River. Under controlled conditions, we aimed to provide more robust estimates of mean *D. r. bugensis* filtration rates at our study site. In the context of this PhD project, it was a final contribution to assessing potential impacts of suspension feeding by *D. r. bugensis* in the known UK range.

Pilot Study 3 - *Investigating D. r. bugensis* filtration rates of natural stream water in controlled laboratory flume conditions.

Studies have measured the laboratory filtration rates of a variety of suspension feeding freshwater taxa and associated depletion of seston (e.g. Shumway et al. 1985; Lauritsen 1986; Way et al. 1990; MacIsaac 1992). Lotic species have been typically observed in circulating chambers or experimental flumes (e.g. Cole et al. 1992; Geogrian and Thorp 1992; Denis et al. 1999; Pusch et al. 2001). For *Dreissena* spp., depletion of seston in circular flumes during feeding has been used to estimate total suspended solid (e.g. Schneider et al. 1998), chlorophyll-*a* (Bastviken et al. 1998), phytoplankton (e.g. Roditi et al. 1996), blue-green algae (Vanderploeg et al. 2000), and bacteria (Silverman et al. 1995) clearance rates per individual (unit mg L^{-1} h^{-1}). Such values have been used to estimate *Dreissena* spp. water filtration rates in lentic and lotic freshwater environments (e.g. Reeders 1989; Fanslow et al. 1995; Strayer et al. 1999; Garnier 2000; Madenjian 2011).

While Reeders et al. (1989) suggested laboratory derived filtration rates could be problematic due to abnormal *ex-situ* behaviours, preventative efforts may be made to create more

naturalistic conditions *ex-situ* for test organisms. With *Dreissena* spp. for example, estimates have been calculated from seston depletion in natural river water rather than artificial algal cultures (e.g. Dioniso-Pires 2004; Fanslow et al. 1995), which could provide food quality different to found *in situ*. Efforts have also been made to create hydraulic conditions simulative of a test specimen's source stream; such as for Unionidae spp. and Asiatic Clam *Corbicula fluminea* (Ackerman 1999; Pusch et al. 2001). We aimed to follow similar approaches in our study; measuring turbidity (NTU) depletion from *D. r. bugensis* feeding to calculate mean filtration rates per individual (L^{-1} hr^{-1}). Our experiments were undertaken on natural stream water in a laboratory flume system, simulating conditions roughly analogous to found in Wraysbury River.

Methods

Between 26th June and 7th July 2018 we collected experimental materials from Wraysbury River each morning. For the first five days, ten adult *D. r. bugensis* specimens (24-35mm shell length) were retrieved from a site of known *D. r. bugensis* establishment (Lat 51.455889; Long -0.518917) with pond net sweeps. Roditi et al. (1996) suggested the detachment of *Dreissena* spp. from their substrate prior to experimental incubation may lower specimen filtration rates and we chose not to detach mussel shells from their byssus-attached substrate clasts (for example, see: **Chapter 4**; **Figure 4.1**, 85 pp.). Specimens were stored live in a watertight cool box and submersed in 0.5 L^{-1} of stream water for transport back to the laboratory. Approximately $18L^{-1}$ of stream water was also collected in 9 $2L^{-1}$ polyethene containers and inverted at 0.5 stream depth at the centre of the channel, approximately 5m upstream of our *D. r. bugensis* sampling area. Transport back to the laboratory took approximately 1 hour and each experiment run was completed within a further 5 hours in the laboratory. For biosecurity precaution, all *D. r. bugensis* specimens were boiled and disposed of as biological waste at the

end of each experiment. Collected stream water was recollected in the polyethene containers, returned and emptied into the Wraysbury River the following morning. For the second five days we conducted control experiments without *D. r. bugensis* present and did not collect specimens on return to the river because none were needed for the controls.

In the laboratory, experiment runs were conducted in a miniature, circular flume with a tilting channel (dimensions:84 x 10 x 20cm^{-1}) positioned above a base channel (dimensions 93 x 14 x 20cm; **Figure 5.7**). Water circulation through the flume was moderated by a 110w^{-1} ducted propeller pump at the base channel's anterior end. Opposite, a plunging weir could be adjusted to determine stream depth in the overhead channel (**Figure 5.7**). Across the daily experiments, flume settings (pump speed: 40% capacity; plunging weir: 2mm opening) and test methodology was identical.

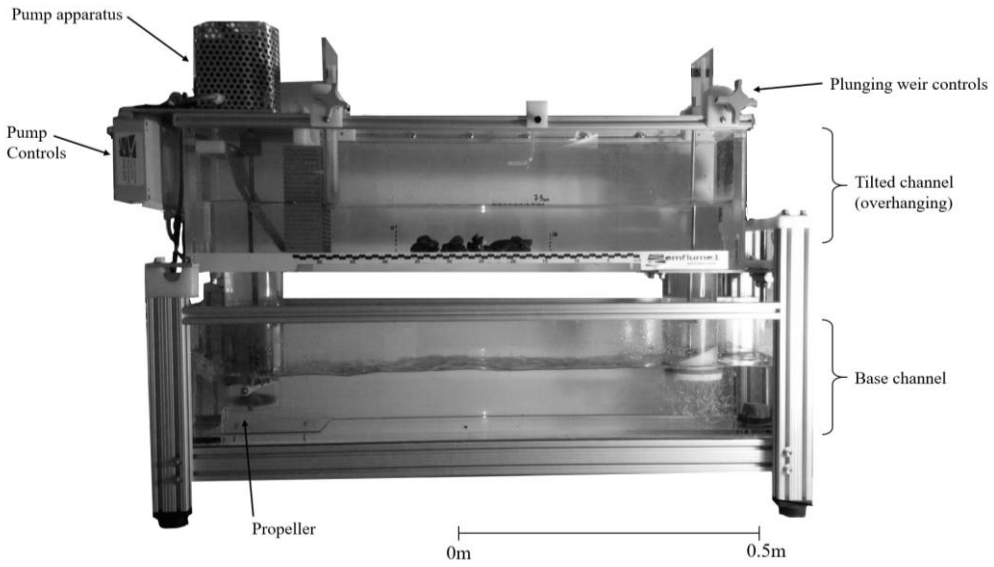


Figure 5.7 Photograph of the Emflume 1 mini flume system with scale and features annotated.

Firstly, 16L^{-1} of stream water was measured and emptied into the flume's base channel with circulation through the system at pre-described settings for a period of 1 hour. This provided time for mixing of natural seston throughout the water column alongside *pre-hoc*

measurements assessing conformity of hydraulic conditions. Halfway down the overhanging channel, we recorded total stream depth (cm) alongside flow *x* velocity (m^{-1} s^{-1}; measured near the top of the water surface) with a Valeport flow meter, using the 30 second average reading. The main experiment was then undertaken with the first five days being treatment tests (with *D. r. bugensis* present) and the second controls (without *D. r. bugensis* present).

For treatment tests, ten *D. r. bugensis* specimens and associated byssus-substrate agglomerates were rinsed with de-ionised water; removing as much loose particulate matter as possible (as: Fanslow et al. 1995). Each mussel and attached byssus-substrate were placed carefully to sit approximately equidistant, 1cm apart, at the centre of the overhanging flume channel (**Figure 5.8a**). Shell orientation was randomised to replicate observations of natural populations in the field. At no point was flow shear stress great enough to transport specimens downstream. After placement, a 1hr acclimatisation period was provided for mussel feeding to commence. This appeared long enough for all *D. r. bugensis* to extend their inhalant and exhalent syphons (See: **Figure 8b**); signifying filtering activity (Sprung and Rose 1988). At any one time during the experiment it was usual to observe all ten mussels feeding and individuals extended syphons in alteration, with 1 to 4 out of 10 not actively feeding.

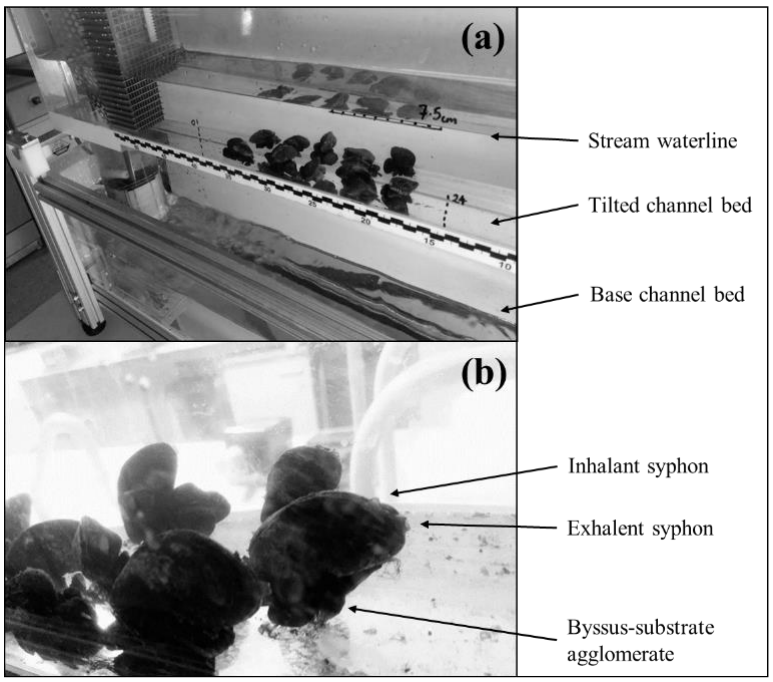


Figure 5.8 Photograph of *D. r. bugensis* specimens (a) arranged on tilted channel bed and (b) with syphons extended.

Following acclimatisation, we commenced a 3 hour measurement phase where stream turbidity was measured at 15 minute intervals. In each case, three replicate sample vials ($10ml^{-1}$) were filled at approximately 0.5 depth at the centre of the flume's base channel, avoiding disturbance of *D. r. bugensis* specimens in the overlying, tilting channel. Water turbidity (NTU) in each vial was immediately measured from samples using a hand held Palintest Turbimeter (PTH092) and emptied back into the base channel. From 60 seconds prior to each measurement, we noted the number of *D. r. bugensis* specimens with extended syphons, alongside the number of pseudofacaes expulsions seen in that time.

Water temperature (^oC), dissolved oxygen (DO; mg L^{-1}), Conductivity (µs cm-1), Total Dissolved Solids (TDS mg L^{-1}) and pH was also measured in the flume's base channel to assess stream conditions and their homogeneity at the start, middle and end of the measurement period (0, 90 and 180mins, respectively). All parameters were recorded using a HACH™ HQ30d multi-probe and HI9811-5N pH/EC/TDS/°C portable meter. For comparison, we considered records of physicochemical conditions in the Wraysbury River collected by the UK Environment Agency across March to May 2018, showing mean values of Dissolved Oxygen 10.0 ± 0.6 SE, Conductivity 902 µs cm^{-1} ± 66 SE, and Alkalinity 220 mg L^{-1} as CaCO3 ± 0.6 SE (**Appendix IV**; 274 pp.). Flume water temperature was maintained between 20-21^oC during each experiment, matching ambient laboratory temperature. We finally collected a second set of measurements for total stream depth alongside longitudinal velocity at the end of each experiment. Like for our physicochemical measurements, comparisons were made with those taken at the experiment's start to assess homogeneity of conditions within the measurement phase.

Analysis

Mean NTU concentrations over the 3hr incubation time were summarised graphically for treatment and control experiments. For each of our treatment experiments, a mean Filtration rate (FR) per *D. r. bugensis* individual was calculated for NTU units according to the equation from Coughlan (1969):

$$FR = \frac{Vol\ [(\ln T_0 - \ln T_1) - [(\ln T'_0 - \ln T'_1)]}{t} \div n$$

Equation 2.

Were, FR= Mean filtration rate of *D. r. bugensis* individuals per experiment, Vol= volume of river water in flume ($16L^{-1}$), t=time ($3h^{-1}$), T_0= Initial NTU measure for *D. r. bugensis* treatment flume run, T_1= final NTU measure for *D. r. bugensis* treatment flume run, T'_0= initial NTU measure for control flume run, T'_1= final NTU measure for control flume run and *n*= the number of *D. r. bugensis* specimens in the flume.

However, our treatment and control experiments were collected on different days and could not be strictly paired. As such, we incorporated an average value of NTU reduction during our control tests (as for: Diggins 2001). Equation 2 was rewritten with the term $\bar{C}$, representing the mean difference of the natural log of NTU between initial and final measurements across all control tests:

$$FR = \frac{Vol\ (\ln T_0 - \ln T_1) - \bar{C}}{t} \div n$$

Equation 3.

Results

Stream physicochemical conditions appeared homogenous throughout the duration of our flume experiments. The range of values recorded for dissolved oxygen, pH, conductivity, temperature and total dissolved solids within treatments appeared small. Means for each parameter within and between treatments were associated with low standard error (**Table 5.5**). Flume hydraulic conditions similarly appeared analogous throughout our experiments. Stream depth was consistent across all experiments while the range of flow velocities within and across treatments were very small. Mean values for flow velocity (m^{-1} s^{-1}) across all treatments presented low standard error (**Table 5.5**).

Table 5.5 Range and mean values (± SE) for stream physicochemical and hydraulic parameters in the flume at the start and end of control and 10 *D. r. bugensis* treatment tests.

Parameter Measured	Range *all measures*	Mean +SE *all measures*	Range *all measures*	Mean +SE *all measures*	Range *all measures*	Mean +SE *all measures*
	Control treatments		10 *D. r. bugensis*		Both treatments	
Dissolved oxygen **mg L^{-1}**	5.0 - 6.1	5.3 ± 0.06	4.1 - 6.0	4.9 ± 0.1	4.1 - 6.1	5.1 ± 0.1
pH	8.5 - 8.6	8.6 ± 0.04	8.3 - 8.5	8.4 ± 0.02	8.3 - 8.6	8.5 ± 0.01
Conductivity **µS cm^{-1}**	790 - 826	815 ± 1.9	790 - 861	816 ± 3.6	790 - 861	816 ± 2.0
Temp **^{o}C**	20.7 - 21.9	21.6 ± 0.07	20.8 - 22.3	21.6 ± 0.1	20.7 - 22.3	21.6 ± 0.01
Total Dissolved Solids **TDS**	412 - 441	426 ± 2.3	416 - 441	428 ± 1.8	412 - 441	427 ± 1.5
Flow **m S^{-1}**	0.22 - 0.23	0.23 ± 0.003	0.22 - 0.23	0.23 ± 0.001	0.22 - 0.23	0.23 ± 0.002
Stream depth **cm^{-1}**	7.5 - 7.5	7.5 ± 0	7.5 - 7.5	7.5 ± 0	7.5 - 7.5	7.5 ± 0

For our *D. r. bugensis* treatment runs, mean stream turbidity (NTU) was shown to decline over the 3 hour measurement period. In each case, starting NTU decreased by between 1-3 units during the run. Standard error for each 15 minute mean was moderate across all experiments and in most cases, NTU declined consistently. Only on June 28th was NTU shown to rise above starting values after commencement of the experiment (**Figure 5.9a**). For the control runs, mean stream turbidity (NTU) was also shown to decline over the 3 hour measurement period, but to a lesser rate than for the *D. r. bugensis* treatments. Within the control runs, starting NTU

was mostly shown to decrease by 0-1 NTU during the measurement period, however the final 7th July experiment presented a more significant reduction of 1-2 NTU. In all control runs, NTU was shown to rise above starting NTU values at least once after the commencement of the experiment (**Figure 5.9b**).

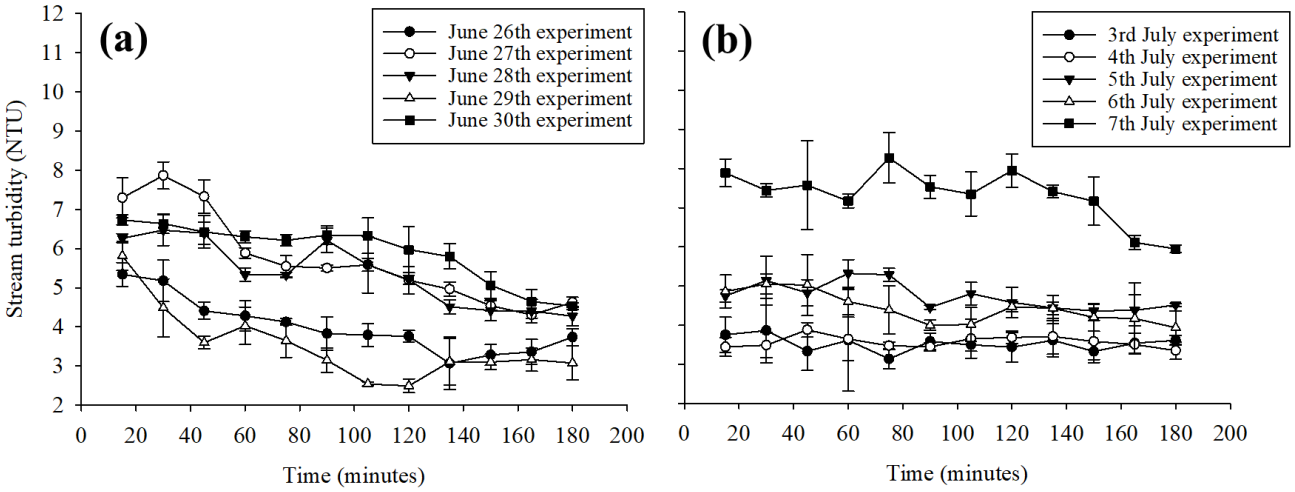


Figure 5.9 Mean stream turbidity measurements (± SE) through experiment duration (minutes) for (a) *D. r. bugensis* treatment runs and (b) control runs.

At any one time, all *D. r. bugensis* individuals in our treatment runs were not observed to be actively filtering. The mean number of feeding *D. r. bugensis* during the measurement periods was 8.2 individuals, ranging from 7.7 – 8.8 across runs. Estimated filtration rates per *D. r. bugensis* individual were calculated using **equation 3** for different treatment runs, incorporating (for *n*; **Equation 3**) mean *D. r. bugensis* individuals feeding throughout the corresponding measurement phase. The mean difference of the natural log of NTU between starting and end measurements across all control runs ($\bar{C}$; **Equation 3**) was 0.122. *D. r. bugensis* filtration rates appeared to vary across all tests in a range from 0.157 – 0.316 L^{-1} NTU per individual hr^{-1}. Mean filtration rates across all treatment runs was 0.210 L^{-1} NTU per individual hr^{-1} ±0.07 SE (**Table 5.6**).

Table 5.6 Mean filtration rate, number of feeding *D. r. bugensis* and rate of *D. r. bugensis* psudofacaes expulsions observed per *D. r. bugensis* treatment experiment.

Experiment Date	Filtration rate per *D. r. bugensis* individual (L^{-1} NTU hr^{-1})	Mean no. feeding *D. r. bugensis* (± SE)	Mean psudofacaes expulsion rate (± SD)
June 26th 2018	0.161	7.8 ± 0.6	1.4 ± 0.5
June 27th 2018	0.232	7.7 ± 0.7	1.5 ± 0.5
June 28th 2018	0.157	8.8 ± 0.5	1.1 ± 0.5
June 29th 2018	0.316	8.7 ± 0.5	1.3 ± 0.8
June 30th 2018	0.182	8 ± 0.6	1.2 ± 0.7
Overall Mean (± SD) :	0.210 ± 0.07	8.2 ± 0.6	1.3 ± 0.6

Discussion

In this third pilot study, mean filtration rate per *D. r. bugensis* individual (0.210 L^{-1} NTU hr^{-1}) was found to be near the centre of the range reported for *Dreissena* spp. in the literature (0.114 - 0.309L^{-1} hr^{-1}; Roditi et al. 1996; Diggins 2001). While laboratory effects may reduce comparability of our results to the natural environment (Ikeda 1977; Reeders et al. 1989); flume conditions appeared some what analogous to those in Wraysbury River. For example, across tests, mean values for stream flow (0.2 m^{-1} s^{-1}), temperature (21^{o}C), conductivity (800us^{-1} cm^{-1}), pH 8.7, total dissolved solids (TDS) and dissolved oxygen (5.1 DO mg^{-1} L^{-1}) were comparable to monitoring records from the UK Environment Agency for March – May 2018 (**Appendix IV**; 274 pp.). Although other *in situ* influences on mussel activity such as such as diurnal trends (Horgan and Mills 1997), suppression by predation (Kobak 2010) and stream flow variation (Ackerman 1999) were not accounted for in our study; estimations may provide more contextualised indications of filtering capacity for *D. r. bugensis* in Wraysbury River.

Returning to calculations made in pilot study 2 (See: **equation 1**; 136 pp.): *D. r. bugensis* feeding at this rate (0.210 L^{-1} NTU hr^{-1}) would require densities of 1044 individuals m^{-2} to filter 10% of the water volume in a reach 60m long with a 5.3m^{-1} wide channel and steady stream discharge of 0.44m^{-3} s^{-1} (as recorded therein). While the maximum mean *D. r. bugensis* density found in Wraysbury River was only 376 individuals m^{-2}; this magnitude, if continuously distributed down an analogous stream, could have theoretically filtered 100% of the transient water volume over a distance of 2km. Further, densities equivalent only to 54 individuals m^{-2}, (as recorded in 2015-16 for the wider invaded reach in **Chapter 2** (See**: Table 5.1**), could filter 15% over 2km. While again, such highly simplified calculations (i.e. using a steady flow rate, homogonous channel morphology and continuous *D. r. bugensis* distribution) can only be indicative; they suggest *D. r. bugensis* would impact downstream seston concentrations over longer sections of the Wraysbury River; particularly if higher population densities of the invasive developed over time.

To further assess potential impacts of *D. r. bugensis* suspension feeding in UK rivers, additional understanding of the species' capacity to reach certain densities across different lotic habitats will be needed. It has been noted that *D. r. bugensis* establishment in shallow, lotic rivers like the Wraysbury River was unexpected (Lucy et al. 2008; Alridge et al. 2014) and the ability of the species to reach critical densities (i.e. for significant filtration of water volume) in such environments is unknown. This is of interest because in smaller streams, associated with lower transported water volumes, the theoretical densities of *D. r. bugensis* required to filter significant proportions of the water column would be lower. Further, systems associated with lower discharge rates could be more vulnerable to suspension feeding impacts of *D. r. bugensis* due to increased water residence times (*sensu* Dame 2012). Additional study could examine *D. r. bugensis* habitat preferences across different lotic habitats to help assess their potential densities in uninvaded rivers. See **Chapter 7**; 179 pp. for progress in this area.

Estimates of potential mussel density, coupled with contextualised feeding rate estimations for different UK rivers could allow the development of impact models for *D. r. bugensis* feeding. Other European studies have aimed to achieve this for different species, such as for Pigneur et al. (2013); where laboratory derived *C. fluminea* filtration rates were applied to a bathymetric simulation of the Belgian River Meuse. Here, it was estimated a 70% loss of annual phytoplankton biomass would occur in invaded reaches. In a similar study, Descy et al. (2003) coupled *D. polymorpha* density estimates from the field (collected by Bachmann et al. 1995) with literature filtration rates to model impacts on specific phytoplankton taxa in the French River Moselle (phytoplankton growth model adapted from Everbecq et al. 2001). Here, significant losses of common diatom taxa *Stephanodiscus* spp. and *Skeletonema* spp. were predicted given present densities of the mussel. While our third pilot study on *D. r. bugensis* was of limited scope, greater repetition could derive more robust feeding rates for the species and contribute to similar models for UK freshwaters. Progress in these areas could provide an opportunity for more robust predictions for *D. r. bugensis* feeding impacts in UK rivers.

General Conclusions

1. *Dreissena* spp. are well adapted suspension feeders which may form large population densities in varied freshwater environments. They have been shown to heavily graze seston in lentic and lotic water bodies at various scales. Studies associate this with phytoplankton, zooplankton and water turbidity reductions in invaded systems. Resulting sunlight penetration and benthic enrichment from pseudofacaes expulsion may facilitate cohabiting macrophyte and periphyton communities. Secondary facilitation of benthic macroinvertebrates has been associated with consumption of *D. r. bugensis* pseudofacaes and increased periphyton density; though cohabiting suspension feeders could face food competition.

2. Problematically, much contributory research on *Dreissena* spp. suspension feeding has been undertaken in lake systems or large, North American rivers. Potential suspension feeding impacts of the new UK species, *D. r. bugensis*, may be uncertain in smaller, UK lotic environments like the Wraybusry River (where *D. r. bugensis* was first confirmed). Progress in understanding mussel suspension feeding impacts in such systems will enable better predictions of *D. r. bugensis* impact potential across UK rivers.

3. Confounding factors for downstream seston depletion have made assessment of suspension feeding impacts in lotic environments difficult. For example, allocthonous and autochthonous inputs within an invaded reach may counteract removals by grazing. High stream discharge rates could provide insufficient time of water exposure to significant seston loss. Rivers with lower discharge, reduced auto and allocthonous seston input and higher *Dreissena* spp. densities are as such, likely to be most vulnerable to suspension feeding impacts. For more robust prediction of the impact potential of *D. r. bugensis* filter feeding across river typologies; efforts should be made to assess habitat preferences of the species, allowing better prediction of potential densities under different conditions.

4. Future work on suspension feeding impacts in lotic environments could take advantage of recent advances in low cost environmental monitoring and data collection technologies. In particular, the use of low cost logging platforms such as Arduino (see: Lockridge et al. 2016) may provide high resolution turbidity monitoring as river sondes. Variation in turbidity-inferred seston concentrations upstream and downstream of suspension feeding communities could be monitored at greater resolution than for previous literature. Across long temporal scales, continuous logging with this approach could elucidate the impacts of suspension feeders like *D. r. bugensis* in UK rivers while clarifying confounding background fluxes of seston in the natural environment.

5. Though an understudied factor for suspension feeder impacts, water column mixing may be an important determinant for the influence of *Dreissena* spp. grazing in rivers. In a poorly mixed stream, refiltration near the bed is more likely to occur and theoretically, grazing pressure will disproportionately impact the benthos, where filtration occurs. This suggests seston depletion would be concentrated closer to the benthic community and cohabiting filter-feeding invertebrate taxa, (including *D. r. bugensis*) may be limited under conditions of high grazing. The potential for longitudinal self-limitation of *D. r. bugensis* in lotic environments (due to food competition) should be an important priority for further study. Elucidating this issue may improve predictions of *D. r. bugensis* feeding impacts in UK rivers.

6. Hydraulic pressures in streams, absent in lakes, could suspend mineralogic seston at rates that counteract filtration by *Dreissena* spp.. Resultingly, mean turbidity reductions associated with other *Dreissena* spp. invasions in the literature could be more subdued in lotic environments. It follows aforementioned impacts such as the facilitation of macrophyte and biofilm growth (due to increased solar penetration) would be limited in rivers with high mineralogic suspension rates. Secondary benefits for certain benthic invertebrates may correspondingly be reduced in such cases. Future work *in situ* should ensure more detailed assessment of silt availability to account for this factor.

Chapter 6. Investigating 'Invasional Meltdown' in freshwaters driven by *Dreissena* spp.

Summary:

Under 'Invasional Meltdown Hypothesis' (IMH; *sensu* Simberloff and Von Holle 1999) the establishment of one invasive species facilitates that of another. While mechanisms to explain such processes may vary across taxa groups and environments; complimentary interspecies relationships have been evidenced by invasion biologists. A commonly cited example has been commensality of the invasive freshwater bivalve *Dreissena* spp. and other Ponto-Caspian taxa; particularly amphipod *Dikerogammarus* spp.. However, some studies report uncertainty whether post establishment, *Dreissena* spp. especially benefit other Ponto-Caspians or provide generalistic facilitation across a range of both native and invasive taxa. The recent expansion of *Dreissena rostriformis bugensis* to UK freshwaters necessitates studies to elucidate this matter.

A littoral benthic survey was undertaken in Barton Broad, Norfolk; one of the few UK freshwater environments where the known range of *Dreissena* spp. and *Dikerogammarus* spp. had overlapped since 2010. Study design tested associations of benthic invertebrate taxa with live and dead *Dreissena* spp. alongside various physicochemical bed characteristics. Results suggested that benthic invertebrates in Barton Broad were strongly influenced by the presence of *Dreissena* spp., with clear variations in community composition among site groups categorised by different mussel densities. The distribution and abundance of Ponto-Caspian and prominent native taxa showed contrasting responses to increasing *Dreissena* spp. density. Amphipod *Dikerogammrus* spp. were strongly, positively associated with both live and dead *Dreissena* spp. shells; whereas both Oligochaeta spp. and Chironomidae spp. negatively so. In particular, the negative response of Chironomidae spp. to *Dreissena* spp. mussel beds was surprising because this taxa group had shown positive relationships in other invaded environments. It was considered that *Dikerogammarus* spp. could predate Chironomidae spp. on mussel beds, precluding this niche opportunity. While that mechanism was not proven by this study, results did support a model of species-specific rather than general facilitation in Barton Broad.

Further, facilitation of *Dikerogammarus* spp. by *Dreissena* spp. was heavily implied by the results of this study, underlining the risk of Invasional Meltdown processes following *Dreissena* establishment in UK freshwaters. Future work should aim to elucidate specific mechanisms of commensality between *Dreissena* spp. and other Ponto-Caspians. In addition, investigations into which types of invaded environments were most liable to similar community structuring by *Dreissena* would progress knowledge in this area. In relation to the wider thesis, this study indicated establishment of another *Dreissena* spp. species in the UK could increase the risk of further Ponto-Caspian invasions where established.

Introduction

Ecological impacts of invasive species have been largely assessed through measures of change to native biological communities (Richardson and Pyšek 2006; Rodriguez 2006). However, the importance of interactions among invasive species was highlighted by Simberloff and Von Holle (1999), with the introduction of 'Invasional Meltdown Hypothesis' (IMH). Authors suggested pioneer invasive taxa can facilitate the establishment of others by creating conditions favourable for propagules of new non-natives (Ricciardi et al. 2001; Gallardo and Aldridge 2014; Braga et al. 2018). As a mechanism of increased risk for invasive establishments, IMH differed from a previously favoured concept of 'biotic resistance' (*sensu* Chapman 1931). For the biotic resistance model, successful invasions were positively associated with reduced species richness in recipient environments (Stachowicz et al. 1999). In contrast, under IMH, the establishment of one invasive species (initially adding to community species richness) would subsequently increase the likelihood of other successful invasions (Ricciardi 2001; Simblerloff 2006). Their risk, exponentially increasing through time, resulting with a runaway 'meltdown' effect (Gallardo and Aldridge 2015).

A series of studies have since reviewed evidence for IMH (e.g. Ricciardi 2001; Richardson and Pyšek 2006; Simberloff et al. 2006; Jeske et al. 2012) with considerable attention given to the theory in scientific and public discourse (Simberloff et al. 2006). While arguments persist regarding the applicability of IMH across a range of environments and taxonomic groups (Wonham and Pachepsky 2006; DeVanna et al. 2011; Jeschke et al. 2012); several studies have shown commensal interactions between pioneer and newly established invasive species (Simberloff et al. 2006). For terrestrial environments, examples include seed dispersal for Macronesian shrub *Myrica faya* by Japanese white eye *Zopsterops japonicus* in Hawaii (Woodward et al. 1990), herbivory of native flora facilitating a competitive invasive weed

Alternanthera philoxeroides by South American snail *Pomacea maculata* in North America (Meza-Lopez and Siemann 2015) and provision of habitat refugia by Philippine orchid *Spathoglottis plicata* nectaries for South African ant *Solenopsis invita* in Puerto Rico (Ackerman et al. 2014). In aquatic environments, examples include vectoring of North American fungus *Aphanomyces astaci* (Alderman et al. 1990) by coevolved crayfish *Pacifastacus leniusculus* in the UK (Alderman et al. 1990), provision of shell habitat for Asian anemone *Diadumene lineata* by Asian hornsnail *Batillaria attramentaria* in the American Pacific (Wonham et al. 2005) and vegetative propagation of Eurasian milfoil *Myriophyllum spicatum* via the shredding behaviour of the central American crayfish *Orconectes rusticus* in Canada (Maezo et al. 2010). Across this literature a further, regularly cited example of a pioneer invasive under IMH has been *Dreissena polymorpha* (Pallas 1771), the Ponto-Caspian zebra mussel (e.g. Ricciardi and MacIsaac 2000; Ricciardi 2001; Devin et al. 2003; Sousa et al. 2009).

Possible commensalism between invasive *D. polymorpha* and other non-natives has been suggested for freshwaters of the North American Great Lakes region (e.g. Ricciardi and MacIsaac 2000; Ricciardi 2001), continental Europe (Devin et al. 2004; Leuven et al. 2009) and the UK (Gallardo and Aldridge 2013; Gallardo and Aldridge 2015). While clear demonstration of processes by which interactions occur remain lacking (Simberloff 2006; Fridley et al. 2007; Jeschke et al. 2012), experimental studies have suggested that laboratory populations of other Ponto-Caspian species respond positively to *D. polymorpha*. For example, amphipods of *Dikerogammarus* spp. have shown preferential habitation of mussel shell structures in mesocosm experiments (Kobak and Zytkowicz 2007; Kobak et al. 2009) alongside the utilisation of mussel pseudofacaes (Gergs & Rothaupt 2008) and byssal thread (Platvoet et al. 2009*b*) as food resources. In addition, *Dikerogammarus* spp. have shown camouflage patterning characteristic of *Dreissena* spp. shell pigment (Magwick and Aldridge 2011; MacNeil et al. 2012) and in the presence of mussels, perform more effectively than native

amphipods under predation pressure from benthivorous fish (Kobak et al. 2014). It has been suggested that interactions of Ponto-Caspian taxa with *D. polymorpha* occur due to adaptive, co-evolutionary processes (Kobak and Zytkowicz 2007). However, *in-situ* studies of invaded environments debate as to whether *Dreissena* spp. particularly benefit other Ponto-Caspians and to what extent generalistic facilitation occurs across a wide range of native and invasive taxa (DeVanna et al. 2011). Notably, a 'general facilitation' model would not support IMH in the sense of Simberloff and Von Holle (1999), where by principle non-native species should be especially advantaged.

Work to elucidate whether 'general facilitation' or an 'IMH' model can be used to describe the influence of *Dreissena* spp. on benthic ecology in UK freshwaters is unfortunately timely due to recent species invasions. The Ponto-Caspian amphipods *Dikerogammarus villosus* (Sowinsky 1894) and *Dikerogammarus haemobaphes* (Eichwald 1841) were first recorded in the UK in 2010 and 2012, respectively (MacNeil et al. 2010; Constable and Birkby 2016). Considering possible deleterious impacts by *Dikerogammarus* spp. on native invertebrates (Dick and Platvoet 2000; Dick et al. 2002; van Riel et al. 2006) and fish (Casellato et al. 2007), concerns have been highlighted that *D. polymorpha*, already widespread in UK freshwaters (Aldridge et al. 2004), will encourage proliferation of *Dikerogammarus* spp. (Gallardo and Aldridge 2015). Recent arrival of a another *Dreissena* spp. to the UK, the quagga mussel (*Dreissena rostriformis bugensis* 1897), also adds to these dynamics (Aldridge et al. 2014). While currently restricted to urban sub catchments of the River Thames, *D. r. bugensis* have replaced *D. polymorpha* in other invaded environments over long time scales (Haynes et al. 2005; Marescaux et al. 2015) and considering close morphological similarity, may provide analogous facilitation of other Ponto-Caspians. Further, the potential for general facilitation of benthic communities by *D. r. bugensis* has already been identified in this project (see: **Chapter 3**; 57 pp.); appearing similar to that for *D. polymorpha* shown elsewhere (see: Stewart and

Haynes 1994; Ward and Ricciardi 2007; Strayer et al. 1999). Whether *Dreissena* spp. may particularly advantage other Ponto-Caspian non-natives, compared to native taxa, has yet to be investigated *in situ* for the UK.

To improve the current state of knowledge on interspecies impacts of *Dreissena* spp., the aim of this chapter was to compare the degree Ponto-Caspian amphipods and cohabiting benthic fauna were positively associated with *Dreissena* spp. mussel beds in a UK freshwater environment. In determining whether Ponto-Caspian invaders presented particularly strong positive associations with *Dreissena* spp. compared to other benthic fauna, we hoped to elucidate the potential of *Dreissena* spp. as a pioneer species under IMH. To achieve this, we undertook a detailed survey of Barton Broad, Norfolk, one of the few UK environments where the invasive range of *Dikerogammarus* spp. and *Dreissena* spp. had been known to overlap since 2010 (NNSS 2012). In the context of our wider project, we hoped our study would indicate whether further establishment of the new *Dreissena* species, *D. r. bugensis*, could increase risk of an invasional meltdown in UK freshwaters.

Methodology

A benthic survey was undertaken of Barton Broad, Norfolk, UK (Long: 52.739205, Lat: 1.497049), to compare the degree native and non-native fauna were associated with *D. polymorpha* mussel beds. The invasive range of both *D. polymorpha* and Ponto-Caspian amphipod *D. villosus* were known to overlap at this site (NNSS 2012). Benthic macroinvertebrates and a series of substrate characteristics were sampled at 22, approximately equidistant study sites throughout the Broad's littoral shoreline (**Figure 6.1**). All fieldwork was conducted using a 12ft, single-sail row boat with sample processing completed in the

educational camping and adventure centre at Barton Turf, nr. Neatishead (Long: 52.749400, Lat: 1.489282) between 5th and 20th June 2018.

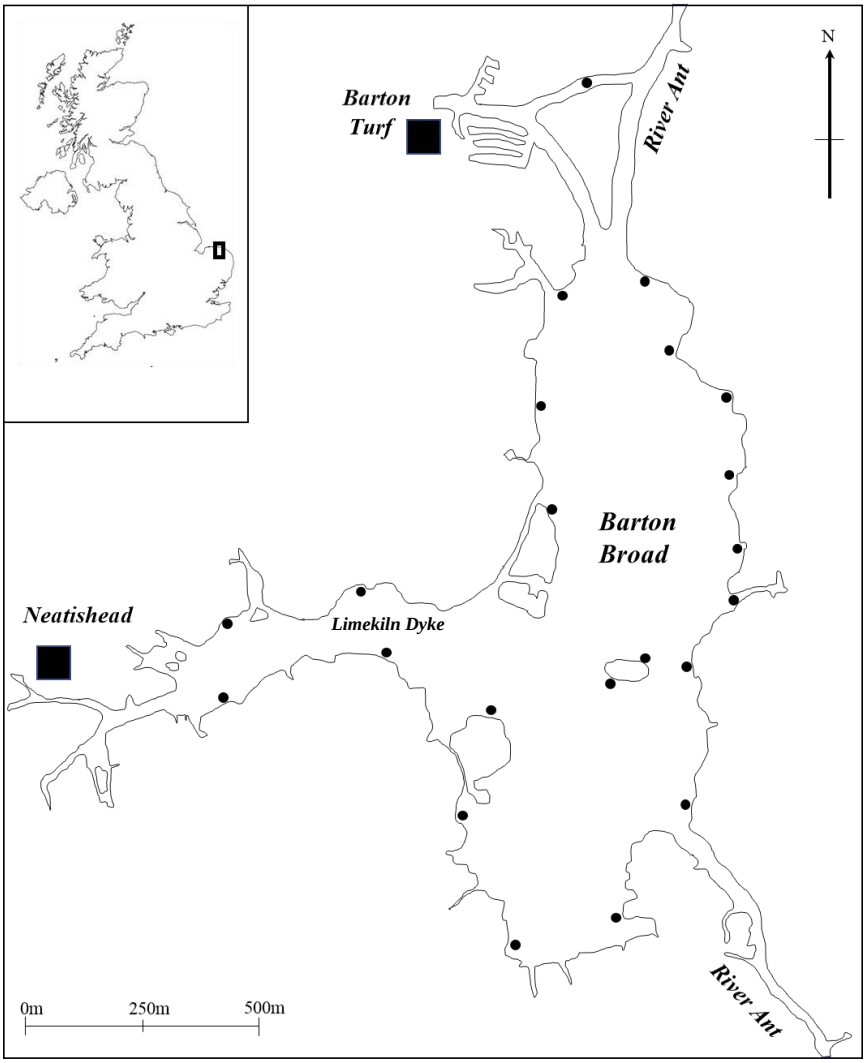


Figure 6.1 Location of the 22 benthic sampling sites in Barton Broad, Norfolk, UK (Long: 52.739205, Lat: 1.497049)

Study Site

Barton Broad is the second largest lentic waterbody in the Norfolk and Suffolk Broads (Osborne 1981) and part of a nationally important wetland network of rivers and lakes (See: Bennion et al. 2001). With an approximate surface area of 700,000m^{-2} and mean depth of 1-2m^{-2} (Osborne 1991); surrounding land uses include nature reserve, boating dockyards, sailing

schools, agricultural fields, scattered deciduous woodland and sparse, village housing. Underlying geology was Breydon formation peats and benthic substrate was known to be predominantly peaty silt (Osborne and Moss 1977; Moss 1980); reflecting the lake's origin as a large medieval peat pit (Lambert et al. 1960; Campbell 1983). Seasonal records collected by the UK Environment Agency between January 2018 and June 2018 gave mean water nutrient concentrations for Barton Broad as total oxidised nitrogen 1.35 N mg L^{-1}, and orthophosphate 0.012 mg L^{-1} with alkalinity as 194 mg L^{-1} as CaCO3 (EA, pers. com. 2018; **Appendix IV** pp. 274).

Data collection

In each of the 22 sites, 5 benthic samples were taken with a petite ponar sampler (model: 1728-G42 EcoEnvironmental Ltd.) lowered to the bed from an anchored, single sailed boat ($3.7m^{-1}$ length, $1.5m^{-1}$ width). The grab device had a sampling area of $231cm^{-2}$ (15.2 x 15.2 cm^{-1}) and weighed $6.8kg^{-1}$, with a self-releasing pinch-pin mechanism. Upon successful collection, samples were lifted from the lake bed and emptied into labelled, $5.6L^{-1}$ polyethene buckets for transport to the laboratory. Samples were subsequently analysed for substrate composition and macroinvertebrates.

Per sample, live macroinvertebrates, dead shells and woody debris were progressively sorted from collected benthic materials using forceps and sorting trays. All macroinvertebrate and dead shell specimens were identified under a high-power ocular microscope to species level except for *Simulium* spp., Hydracarina spp., Ostracoda spp., Oligochaeta spp., and the family Chironomidae. All woody debris and dead shell fragments were separated from mineralogic material by sieving through a mesh size of $4mm^{-2}$. This initial division was used because almost all mineralogic material was composed of silt; however, sand clasts were subsequently separated from silts using a 355 μm^{-2} mesh sieve. No further separation was required as silt

formed the vast majority of collected substrate throughout the survey and at no point were any gravels or larger clasts found. Dead shells, woody debris and the mineralogic substrate components per sample were left to air dry for a standardised period of 24 hours before being individually weighed using portable field scales (model).

Various water physicochemical parameters were measured at each study site with spot samples directly above the point of each ponar grab. Parameters included water pH, dissolved oxygen (DO; mg L^{-1}), conductivity (µs cm^{-1}), temperature (ºC), turbidity (secchi depth cm^{-1}) and water depth (cm^{-1}). Aside from turbidity and water depth, all parameters were recorded using a HACH™ HQ30d multi-probe and HI9811-5N pH/EC/TDS/°C portable meter lowered to approximately 0.5 water depth. Turbidity was determined by measuring the lowered distance of concealment for the sechhi disc (cm^{-1}) while water depth measurements (cm^{-1}) were taken using a marked ranging pole extended into the water from the boat edge. These measurements were taken to test for water homogeneity of physicochemical conditions across sample sites.

Data Analysis

To summarize benthos characteristics per study site we calculated mean macroinvertebrate density (individuals m^{-2}), richness and evenness (Shannon-Weiner index; Krebs 1978). For bed substrate characteristics. We also calculated mean substrate depth and density of live and dead *D. polymorpha*, alongside mean weight of silt, sand, shell and woody debris substrate components (g^{-1}). For descriptive and analytical purposes (see paragraphs below), sites 1-22 were categorised according to mean, live *D. polymorpha* densities with 0, <50, 50 - <400, 400 - <800, and 800+ individuals m^{-2}, corresponding to ‘not present’, ‘low’, ‘moderate’, ‘high’ and ‘very high,’ site groups, respectively. ANOVAs on ranks were conducted to assess variaton of invertebrate summary parameters alongside mean bed substrate characteristics across site categories (non-parametric tests were used due to unequal group sizes). Where significant

variation was found, Dunn's multiple pairwise comparisons were used to elucidate differences between site cateogories.

To assess the direction and strength of correlations between bed substrate characteristics and the 5 most abundant invertebrate taxa found, we conducted Spearman's Rank analysis. Bed substrate characteristics included [1]bed depth from water surface, [2]density of live and dead *D. polymorpha*, alongside weight of [4]silt, [5]sand, [6]shell and [7]woody debris components (g^{-1}) per sample effort. Taxa selected for the analysis were both non-native and native taxa and where significant correlation was found (p = <0.05), we generated scatter plots to demonstrate the strength, direction and slope of each correlation.

Community ordination analyses were used to further summarize benthic fauna composition across sites as grouped by *D. polymorpha* densities (see above). Excluding *D. polymorpha*, the mean density of each taxa was analysed for all sites. Data was Log(X+1) transformed to moderate for the effects of rare or highly abundant taxa (Clarke and Green 1988; Legendre and Gallagher 2001) and all taxa accounting for less than 0.5% of total invertebrate density (across the study) were omitted to reduce distortion of assemblage differences. Analyses were completed using the statistical software package PRIMER-E v.6.1.13; Primer-E Ltd., 2009 (Clarke and Gorley 2006; Clarke 1993; Clarke and Warwick 2001).

Ordination of community structure using Non-Metric Multidimensional Scaling (NMDS) was used to graphically present similarity of benthos composition across sampling sites. Based on Bray-Curtis similarities, this has been a widely used approach for displaying invertebrate community structure data (e.g Kobayashi and Kagaya 2004; Thomson et al. 2005; Ercoli et al. 2015) and applied to assess community composition as weighted by the density of present taxa. A stress function indicated how well the plot summarised distance between mean points for each sampling site, which were shown with symbols according to *D. polymorpha* density

category. Finally, we conducted a similarity of percentages (SIMPER) analysis (Clarke and Warwick 2001) to determine the percentage contribution of different invertebrate taxa towards similarity within study sites grouped by *D. polymorpha* density category. A second SIMPER analysis was then run to assess taxa contributors to dissimilarity between site groups.

Results

Across study sites, the range of water pH (7.6–8.6), dissolved oxygen (5.0–7.9 mg L^{-1}), conductivity (750–841 µs cm^{-1}), total dissolved solids (375–420), Sechii depth (40-84cm^{-1}) and temperature (18.1–20.4 °C) were within norms given the location, geology, seasonal climate and previous monitoring records from the UK Environment Agency (EA., 2018; **Appendix IV** 274 pp.). Overall, measurements showed very similar physicochemical conditions across study sites. Results supported the likelihood that none of these factors would limit the development of similar ecological communities throughout Barton Broad.

Mean lake-wide density of *D. polymorpha* was 242 ± 46 SE, while mean density at sites where present was 554 ± 76 SE. The most abundant *D. polymorpha* populations were recorded throughout the eastern littoral areas of Barton Broad and near the centrally-placed island known locally as 'love island' (**Figure 6.2**. *D. polymorpha* were not recorded near the north eastern or southern shores, while low density populations were found in the westerly Limekiln Dyke and north western littoral (**Figure 6.2**). Five of our 22 study sites could be grouped under the categories of 'high' or ' very high' *D. polymorpha* density; presenting a mean of 685(±154 SE) and 1066(±179 SE) individuals m^{-2}, respectively (**Table 6.1**). Seven sites could be grouped with 'moderate' *D. polymorpha* density (mean of 193 ±33 SE) and four sites under 'low' *D. polymorpha* density (mean of 15.1 ±7.8 SE). *D. polymorpha* were not recorded at six sites (**Table 6.1; Figure 6.2**).

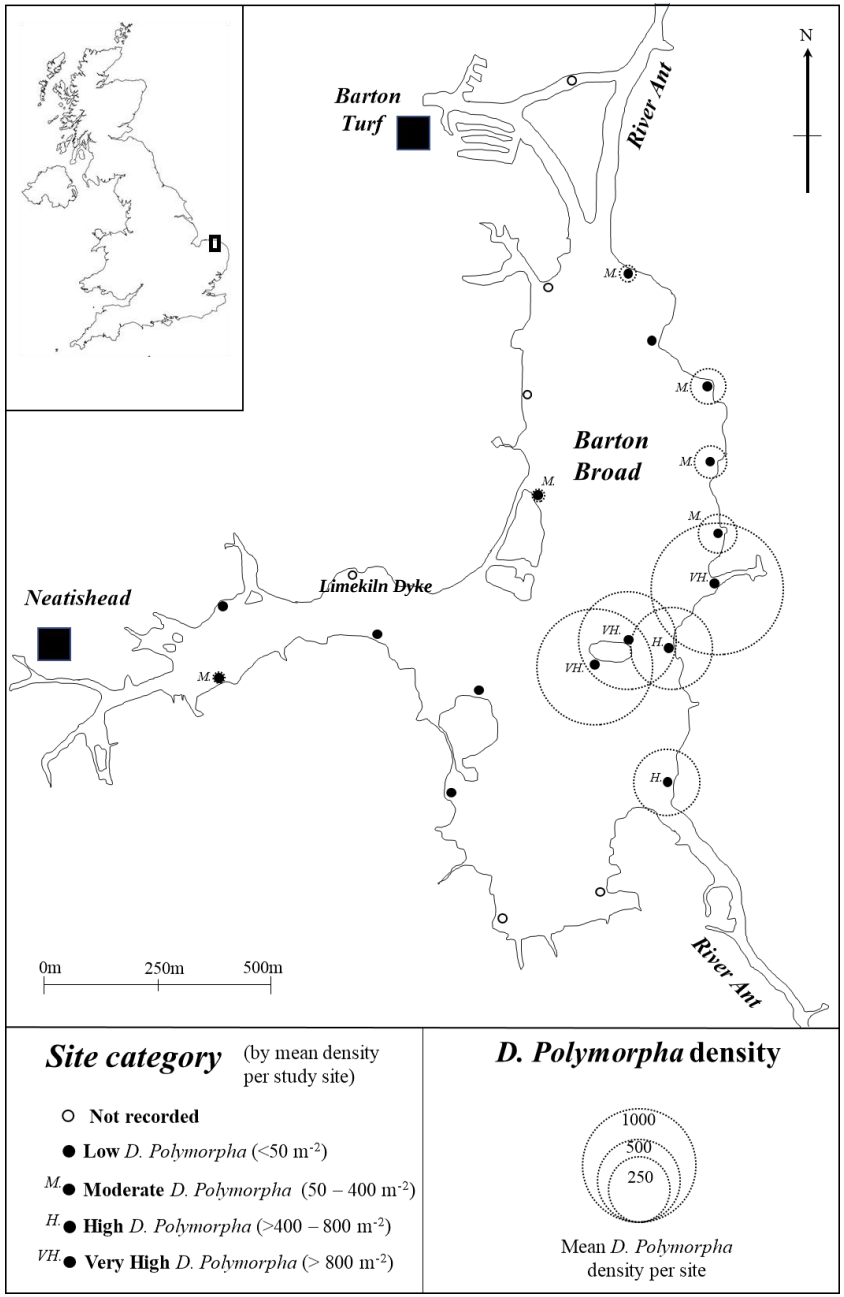


Figure 6.2 Mean *D. polymorpha* density (indivuduals m^{-2}) per site across the littoral perimeter of Barton Broad. Notations include site categorisation according to mean *D. polymorpha* density.

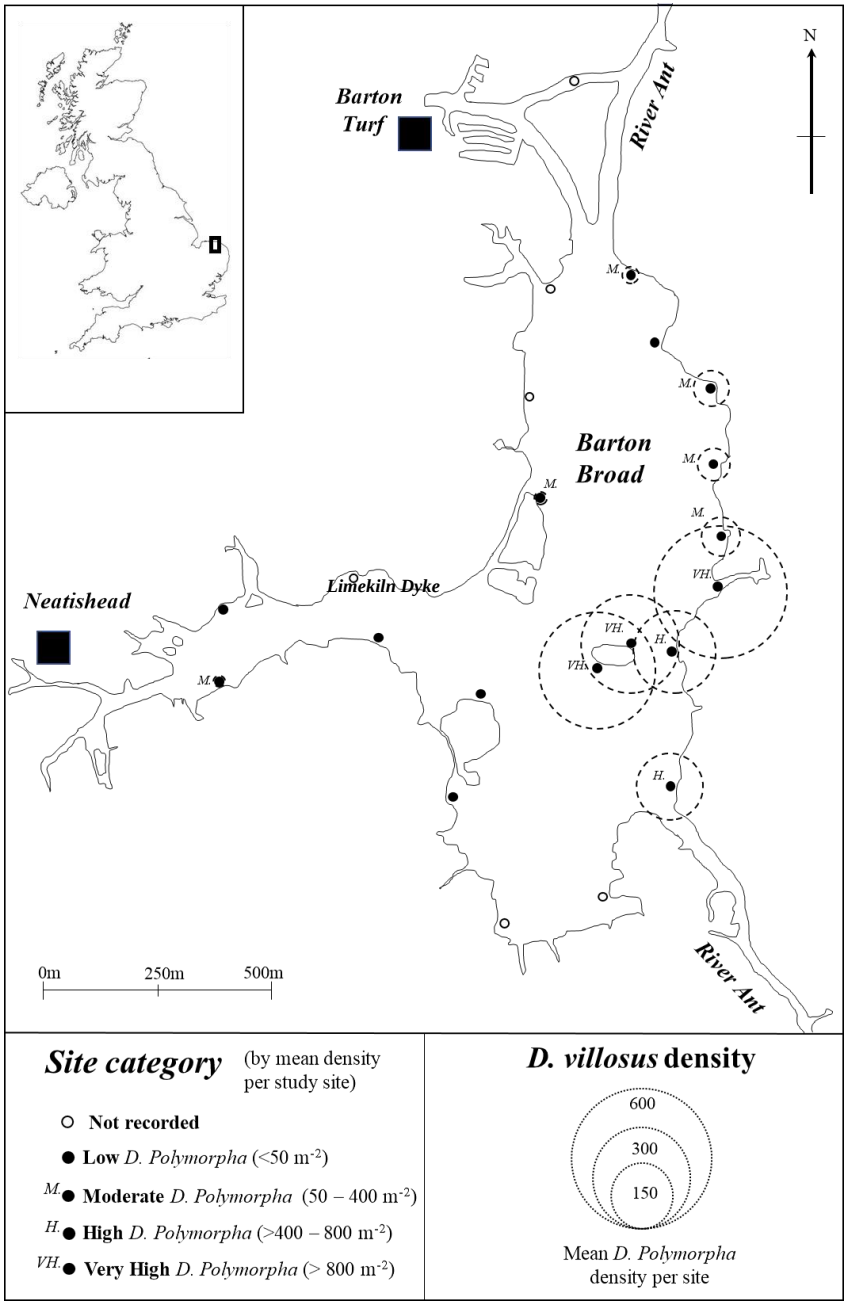


Figure 6.3 Mean *D. villosus* density (individuals m^{-2}) per site across the littoral perimeter of Barton Broad. Notations include site categorisation according to mean *D. polymorpha* density.

Table 6.1 Summary of mean invertebrate community parameters across study sites categorised by live *D. polymorpha* density (mean ± SE). Includes results of 1-way ANOVA on ranks between site categories with Dunn's pairwise comparison test for unequal group sizes.

Parameter measured	Site group mean (± SE) by *D. polymorpha* density (m^{-2})					*Between categories* ANOVA		*Dunn's Test*
	(a) *Not pres.*	(b) *< 50*	(c) *50 - 400*	(d) *>400 - 800*	(e) *> 800*	*Test*	*p - value*	
Total invertebrate density (individuals m^{-2})	430 ± 41	606 ± 73	782 ± 70	1668 ± 302	2049 ± 232	H = 54.4(4)	<0.001	e, d > a, b; e > c; c > a
Density of live *D. polymorpha* (individuals m^{-2})	0 ± 0	15.1 ± 7.8	193 ± 33	685 ± 154	1066 ± 179	H = 80.0(4)	<0.001	e, d > a, b; e > c; c > a
Inverterbate taxonomic richness	3.33 ± 0.27	4.45 ± 0.50	4.89 ± 0.35	6.30 ± 0.40	6.53 ± 0.31	H = 35.5(4)	<0.001	e, d, c, b > a; e > b
Shannon-Weiner Score	0.89 ± 0.081	1.16 ± 0.11	1.24 ± 0.07	1.41 ± 0.09	1.30 ± 0.06	H = 17.8(4)	<0.001	d, e, c > a
no. sites in *D. polymorpha* density category:	*6*	*4*	*7*	*2*	*3*	*N/A*	*N/A*	*N/A*

We found clear differences in overall invertebrate community parameters among site groups (**Table 6.1**). Those with greater *D. polymorpha* populations were associated with increased total invertebrate density, richness and to a lesser extent, evenness (Shannon-Weiner scoring). According to ANOVA on ranks, sites categorised with 'very high' *D. polymorpha* density presented significantly greater mean total invertebrate density compared to all others except the 'high' density site group. Where no *D. polymorpha* were recorded, mean total invertebrate density, taxonomic richness and evenness was significantly lower than for all other site groups except for 'low' density sites (**Table 6.1**; see full taxa list **Appendix II** 269 pp.).

We found strong variation of general bed substrate characteristics across site groups, for which there was a large range in mean silt (g^{-1}; 4.8 - 50.3), woody debris (g^{-1}; 3.6 – 38.2) and shell (g^{-1}; 1.1 – 33.0,) substrate components (**Table 6.2**). According to ANOVA on ranks, site groups with 'high' or 'very high' *D. polymorpha* densities presented significantly reduced mean silt and woody debris components (g^{-1}) alongside significantly increased shells (g^{-1}) compared to the 'low' and 'not recorded' groups (**Table 6.2**). Contrasting findings were clear for the 'low' and 'not recorded' site groups. According to ANOVA, both presented significantly higher mean silt and woody components (g^{-1}) alongside lower shells (g^{-1}) when compared to all other sites (**Table 6.2**). Bed depth from the water surface (cm^{-1}) was the least varied characteristic

between site groups (range: 71 – 103cm^{-1}); with significant differences only driven by shallower water at the 'low' density *D. polymorpha* site category (**Table 6.2**).

Table 6.2 Summary of physical substrate conditions across study sites categorised by mean live *D. polymorpha* density (individuals m^{-2}). Includes results of 1-way ANOVA on ranks between site categories with Dunn's pairwise comparison test for unequal group sizes.

Parameter measured	Site group mean (± SE) by *D. polymorpha* density m^{-2}					*Between categories* ANOVA		*Dunn's Test*
	(a) *Not pres.*	(b) < *50*	(c) *50 - 400*	(d) > *400 - 800*	(e) > *800*	*Test*	*p - value*	
Bed depth from water surface cm^{-1}	96 ± 5.5	71 ± 3.2	97 ± 4.7	103 ± 5.1	90 ± 3.5	H = 18.8(4)	<0.001	b < d, b, a
Density of dead *D. polymorpha* (individuals m^{-2})	36.7 ± 14	163 ± 76	450 ± 105	1014 ± 305	997 ± 183	H = 43.1(4)	<0.001	d, e > a, b; c > a
Substrate Composition silt (g^{-1})	50.3 ± 5.4	36.4 ± 4.3	24.8 ± 5.5	4.8 ± 0.8	5.0 ± 1.0	H = 60.4(4)	<0.001	a, b > d, e; a > c
Substrate Composition shell (g^{-1})	1.1 ± 0.04	3.6 ± 1.6	18.9 ± 3.9	31.0 ± 4.8	33.0 ± 3.5	H = 52.0(4)	<0.001	e, d > a, b; c > a
Substrate Composition woody debris (g^{-1})	38.2 ± 5.1	25.5 ± 3.0	21.1 ± 3.2	4.2 ± 1.6	3.6 ± 1.5	H = 40.4(4)	<0.001	a, b, c > e, d
No. sites in *D. polymorpha* density category:	*6*	*4*	*7*	*2*	*3*	*N/A*	*N/A*	*N/A*

Across all sites, the shell substrate component (g^{-1}) was predominantly composed of dead *D. polymorpha* (range 58 – 94%); except where *D. polymorpha* was not recorded. In this case it formed a lower proportion (mean 28% ±8 SE; **Table 6.3**). According to ANOVA on ranks, a significantly greater percentage proportion of shells at the 'not recorded' *D. polymorpha* site group was from native taxa (mean: 72 % ±8 SE; **Table 6.3**). These included Gastropods *Vivivparus viviparus* (Linnaeus 1758), *Bithynia tentaculata* (Linnaeus 1758), *Radix peregra* (Müller, 1774), *Lymnaea stagnalis* (Linnaeus 1758), *Valvata piscinalis* Müller 1774) and Bivalve *Unio* spp.. Notably, live New Zealand mud snails *Potamopyragus antipodarum* (Gray 1843) were also found in our survey, though dead *P. anitpodarum* shells were not found as a substrate component at any site. Across both 'high' and 'very high' *D. polymorpha* density site groups, the shell component comprised a mean of 77% ±5 SE and 69% ±7 SE of total substrate composition, respectively. This value was clearly reduced for the 'moderate,' 'low' and 'not recorded' site groups with a mean of 34% ±6 SE, 7% ±3 SE and 1.2% ±0.5 SE, respectively (**Table 6.3**).

Table 6.3. Summary of physical substrate conditions across study sites categorised by mean live *D. polymorpha* density (individuals m^{-2}). Includes results of 1-way ANOVA on ranks between site categories with Dunn's pairwise comparison test for unequal group sizes.

Substrate Shell component	Site group mean (± SE) by *D. polymorpha* density m^{-2}					*Between categories* ANOVA		*Dunn's Test*
	(a) *Not pres.*	(b) *< 50*	(c) *50 - 400*	(d) *> 400 - 800*	(e) *> 800*	*Test*	*p - value*	
% *D. polymorpha*	28.4 ± 7.7	57.5 ± 13.8	74.8 ± 5.9	90.2 ± 3.6	93.7 ± 2.4	H = 29.7(4)	<0.001	a < e, d, c
% native Mollusca spp.	71.6 ± 7.7	42.5 ± 13.8	25.2 ± 5.9	9.8 ± 3.6	6.3 ± 2.4	H = 29.7(4)	<0.001	a > c, d, e
% of total substrate composition as shells.	1.2 ± 0.5	6.9 ± 3.4	34.0 ± 6.2	76.5 ± 4.6	68.8 ± 7.2	H = 57.9(4)	<0.001	d, e > a, b; c > a
No. sites in *D. polymorpha* density category:	*6*	*4*	*7*	*2*	*3*	*N/A*	*N/A*	*N/A*

Aside from *D. polymorpha*, the five most abundant invertebrate taxa in the survey were Chrionomidae spp., Oligochaeta, *V. viviparus*, *D. villosus* and *C. curvispinum* (See: **Appendix II** 269 pp.). Cumulatively, these constituted 60% of total invertebrate abundance with Ponto-Caspians *C. curvispinum* and *D. villosus* comprised 26%, alone. According to Spearman's Rank testing, the density of all five most common taxa was significantly correlated with each substrate characteristic except depth from water surface. Strong, positive associations were found for *D. villosus* with both live and dead *D. polymorpha* density, alongside increasing shell substrate component (**Table 6.4**). Notably, the distribution of *D. villosus* in Barton Broad presented clear overlap with that for *D. polymorpha* and the amphipod was not found at sites where the mussel also appeared absent (**Figure 6.3**). Amphipod *C. curvispinum* and gastropod *V. viviparus* showed similar associations to *D. villosus*, though with reduced correlative strength. Alternatively, Chironomidae spp. and Oligochaeta spp. showed a strong, negative correlation with both live and dead *D. polymorpha* density alongside strong positive associations with increasing silt and woody debris substrate components (**Table 6.4**). In contrast, the Ponto-Caspians *D. villosus* and *C. curvispinum* alongside *V. viviparus* presented a strong negative association with each of these parameters (**Table 6.4**).

Scatter plots to further explore significant correlations of the top 5 taxa with various substrate characteristics failed to present linear, binomial or other structured relationships in most cases (**Figure 6.5**). In one exception, *D. villosus* showed a clear, positive, linear relationship with

both live and dead *D. polymorpha* (**Figure 6.4a**) alongside a negative, binomial relationship with increasing silt substrate component (**Figure 6.4b**). In contrast, Chironomid spp. and Oligochaeta presented a clear, negative, binomial relationship with live *D. polymorpha* (**Figure 6.5a**). More generally, native taxa failed to present clearly structured positive relationships with any substrate characteristic (**Figure 6.5**). Scatter plots suggested that aside *D. villosus*, the strongly significant, directional Spearman's Rank correlations (**Table 6.4**) were likely driven by the absence of taxa where certain substrate characteristics predominated.

Table 6.4 Spearman's Rank correlation matrix showing coefficients between the 5 most highly abundant taxa found in Barton Broad and all bed substrate characteristics. Where correlation
is significant (<0.05) coefficients are shown in bold with all p values shown in parenthesis.

Substrate characteristic variables	Five most highly abundant taxa found in Barton Broad				
	D. villosus	*C. curvispinum*	*Chironomidae* spp.	*Oligochaeta* spp.	*V. viviparus*
Density of live D. polymorpha (m^{-2})	**+0.68**** (<0.001)	**+0.59**** (<0.001)	**-0.38**** (<0.001)	**-0.25**** (<0.001)	**+0.36**** (<0.001)
Density of dead D. polymorpha (m^{-2})	**+0.66**** (<0.001)	**+0.39**** (<0.001)	**-50**** (<0.001)	**-26*** (0.001)	**+0.45**** (<0.001)
Sample composition as silt (g^{-1})	**-0.78**** (<0.001)	**-0.49**** (<0.001)	**+0.31*** (0.001)	**+0.38**** (<0.001)	**-56**** (<0.001)
Sample composition as shells (g^{-1})	**+0.76**** (<0.001)	**+0.383**** (<0.001)	**-0.49**** (<0.001)	**-0.316*** (0.001)	**+0.49**** (<0.001)
Sample composition as woody debris (g^{-1})	**-0.63**** (<0.001)	**-0.44**** (<0.001)	**+0.47**** (<0.001)	**+0.324*** (0.001)	**-0.36**** (<0.001)
Substrate depth (m^{-1})	+0.17 (0.730)	+0.05 (0.600)	**-0.20** (0.036)	-0.18 (0.055)	+0.02 (0.828)

In the NMDS plot (stress 0.17), mean community composition across study sites (driven by taxa contributions to total invertebrate density, excluding *D. polymorpha*) showed clear differences in overall community structuring within site groups categorised by *D. polymorpha* density. Sites either without *D. polymorpha* recorded or with 'low' mean densities were clustered tightly to the left of the plot. In contrast, sites with 'high' or 'very high' mean *D. polymorpha* densities were placed to the right. Those with 'moderate' densities were placed more centrally with two sites proximal to the low density group (**Figure 6.6**).

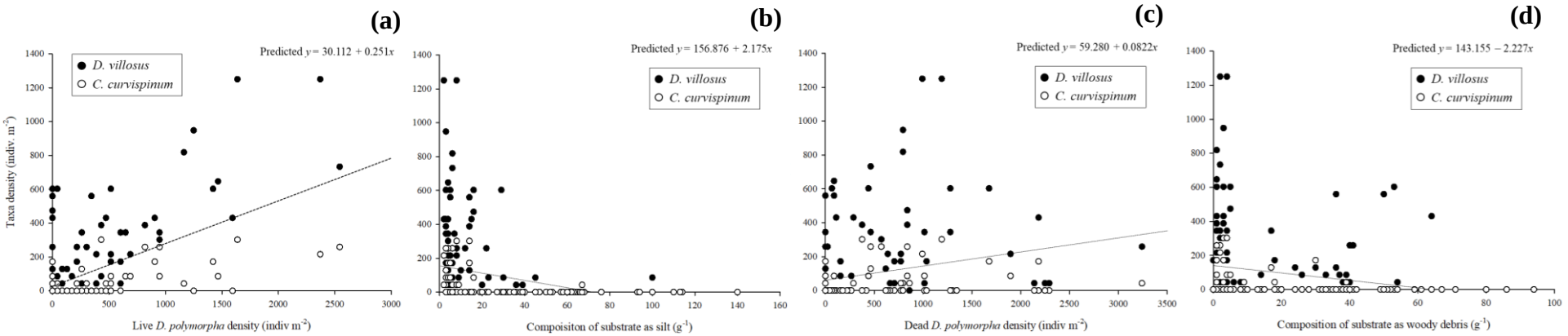


Figure 6.4 Scatter plots presenting correlation of invasive Ponto-Caspian invertebrate density (individuals m^{-2}) with **(a)** live *D. polymorpha* density, **(b)** composition of substrate as silt (g^{-1}), **(c)** dead *D. polymorpha* density and **(d)** composition of substrate as woody debris (g^{-1}) per sample. Linear equation for predicted *y* values and line of best fit through all data also shown.

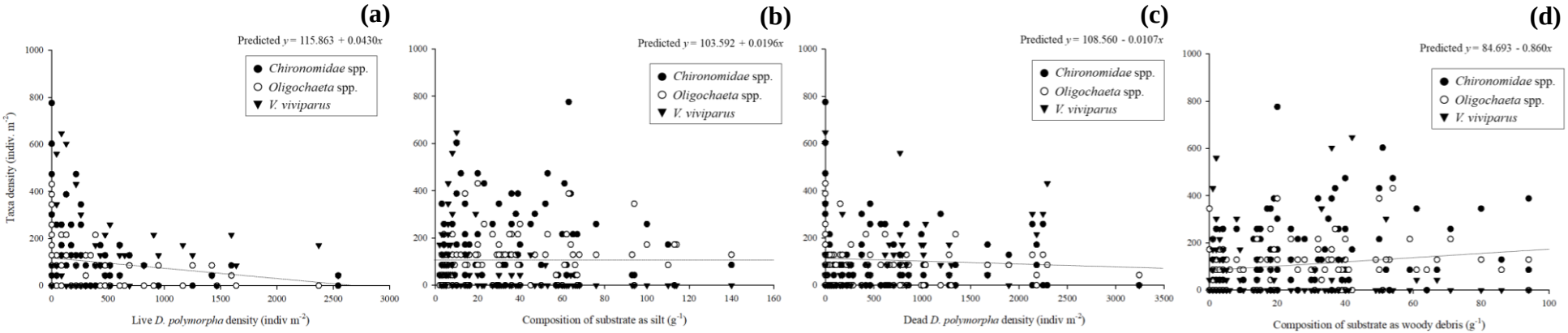


Figure 6.5 Scatter plots presenting correlation of the density (individuals m^{-2}) of the three most abundant native taxa in the study with **(a)** live *D. polymorpha* density, **(b)** composition of substrate as silt (g^{-1}), **(c)** dead *D. polymorpha* density and **(d)** composition of substrate as woody debris (g^{-1}) per sample. Linear equation for predicted *y* values and line of best fit through all data also shown.

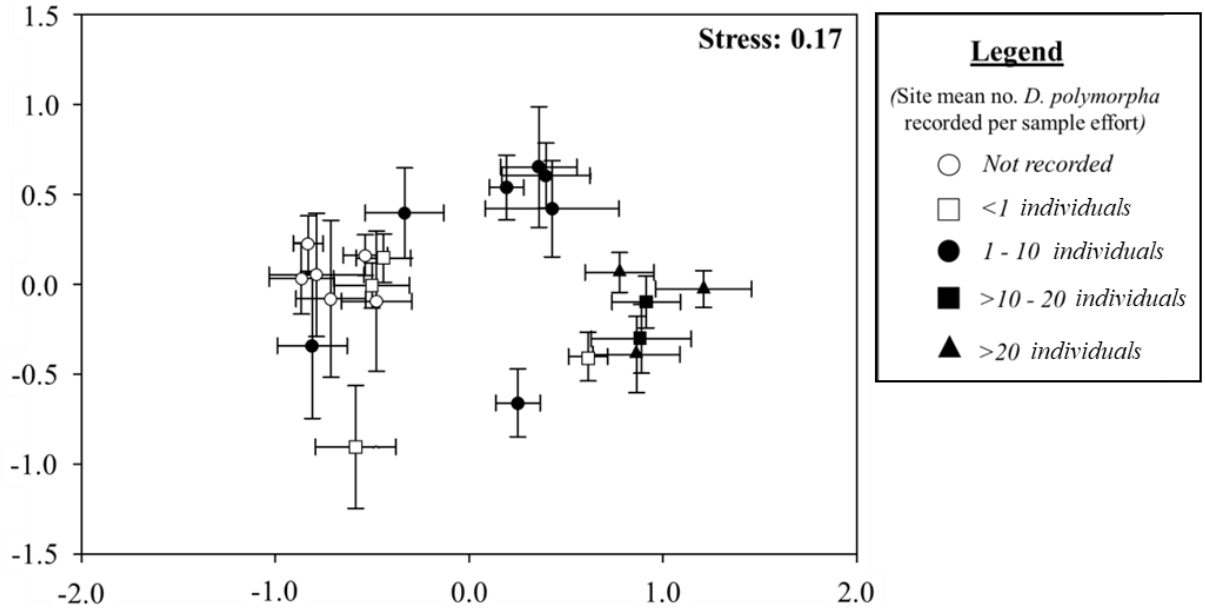


Figure 6.6 Non-metric Multi-dimensional Scaling (NMDS) ordinations of Bray-Curtis similarities in mean community structure per study site (based on proportion of taxa contribution to total invertebrate density; error bars denote Standard Error).

Differences in community composition between site groups were clarified by SIMPER analysis. At all sites categorised by *D. polymorpha* density, within-group similarity was >45% while clear patterns in contributory taxa to community composition in was found in across a gradient of *D. polymorpha* density (**Table 6.5**). For the 'high' and 'very high' *D. polymorpha* density site groups, *D. villosus,* and *C. curvispinum* provided the highest contribution to within site similarity. For site groups with no *D. polymorpha* recorded or 'low' and 'moderate' population densities; the greatest contributory taxa were Chironomidae spp. and Oligochaeta spp. (**Table 6.5**).

Dissimilarity in community composition (excluding *D. polymorpha*) between site groups was smallest between the 'high' and 'very high' *D. polymorpha* density sites. Notably, both showed strong dissimilarity to sites where *D. polymorpha* were not recorded and in each case the taxa *D.villosus*, *C. curvispinum* and *V. viviparus* were the most important drivers of dissimilarity (**Table 6.6**). The 'high' and 'very high' density groups consistently showed >50% dissimilarity

to both ‘low’ and ‘moderate’ density sites; which were predominantly characterised by Chironomidae spp. and Oligochaeta spp. (**Table 6.6**). The sites where *D. polymorpha* were not recorded and those with ‘low’ density populations also presented relatively low dissimilarity (**Table 6.6**); though were at least 50% dissimilar from each other.

Table 6.5 Results of a SIMPER analysis to determine the contribution of important taxa to mean similarity of invertebrate community composition (weighted by the density of taxa present) within site groups categorised by D. polymorpha density (taxa contributing to 95% of cumulative similarity within groups only, excluding D. polymorpha).

Site Group Tested (by *D. polymorpha* density)	*n*	**Mean Similarity (%)**	**Taxa**	**Similarity (%)**	**Cumulative Similarity (%)**
Very High	*3*	**63.29**	*D. villosus*	40.58	40.58
			C. curvispinum	19.67	60.24
			V. viviparus	12.66	72.9
			Oligochaeta spp.	11.87	84.77
			Chironomidae spp.	8.62	93.39
High	*2*	**60.68**	*D. villosus*	44.02	44.02
			V. viviparus	25.26	69.27
			C. curvispinum	13.86	83.13
			Oligochaeta spp.	6.38	89.51
			P. antipodarum	5.61	95.12
Moderate	*7*	**45.76**	Chironomidae spp.	31.95	31.95
			Oligochaeta spp.	28.75	60.69
			V. viviparus	18.49	79.18
			D. villosus	15.15	94.32
Low	*4*	**50.34**	Oligochaeta spp.	52.37	52.37
			Chironomidae spp.	29.71	82.08
			D. villosus	6.69	88.78
			Hydracarina spp.	4.6	93.37
Not Recorded	*6*	**56.34**	Chironomidae spp.	57.27	57.27
			Oligochaeta spp.	34.64	91.92

Table 6.6 Results of a SIMPER analysis to determine the contribution of important taxa to mean dissimilarity of invertebrate community composition (weighted by the density of taxa present) between site groups categorised by *D. polymorpha* density (top 3 taxa only, excluding *D. polymorpha*).

Site Group Tested (by *D. polymorpha* density)	Mean Dissimilarity (%)	Taxa	Dissimilarity (%)	Cumulative Dissimilarity (%)
Very High* vs. *Not Recorded	**69.35**	*D. villosus*	23.69	23.69
		C. curvispinum	16.11	39.81
		V. viviparus	12.15	51.95
Very High* vs. *Low	**57.7**	*D. villosus*	19.95	19.95
		C. curvispinum	16.72	36.67
		V. viviparus	12.44	49.11
Very High* vs. *Moderate	**57.46**	*C. curvispinum*	17.69	17.69
		D. villosus	17.13	34.82
		V. viviparus	11.86	46.68
Very High* vs. *High	**37.46**	Chironomidae spp.	15.52	15.52
		C. curvispinum	14.78	30.3
		Oligochaeta spp.	14.3	44.62
High* vs. *Not Recorded	**76.43**	*D. villosus*	22.53	22.53
		Chironomidae spp.	14.81	37.34
		V. viviparus	14.78	52.12
High* vs. *Low	**63.01**	*D. villosus*	19.35	19.35
		V. viviparus	14.52	33.87
		Chironomidae spp.	14.23	48.1
High* vs. *Moderate	**60.3**	*D. villosus*	17.29	17.29
		Chironomidae spp.	13.74	31.03
		C. curvispinum	13.48	44.51
Moderate* vs. *Not Recorded	**56.67**	*V. viviparus*	17.45	17.45
		D. villosus	15.88	3.3
		Oligochaeta spp.	15.02	48.34
Moderate* vs. *Low	**55.37**	*D. villosus*	16.19	16.19
		V. viviparus	15.76	31.95
		Chironomidae spp.	15.08	47.03
Low* vs. *Not Recorded	**49.8**	Chironomidae spp.	17.64	17.64
		D. villosus	14.07	31.72
		Oligochaeta spp.	13.93	45.65

Discussion

Invertebrate communities in Barton Broad were clearly influenced by presence of *D. polymorpha*. Despite otherwise homogenous physicochemical conditions, distinct variation in community composition was found between sites with different mussel densities. In support of

a model of general facilitation by *D. polymorpha* (*sensu* DeVanna et al. 2011), invertebrate richness and density (excluding *D. polymorpha*) was significantly greater where *D. polymorpha* were more abundant. This was similar to reports from the North American Great Lakes region (Ricciardi et al. 1997; Horvath et al. 1999; Haynes et al. 2005) alongside European lentic (Karatayev et al. 1997; Burlakova et al. 2005; Burlakova et al. 2012) and river systems (Marescaux et al. 2016; Mills et al. *in press*). However, strong segregation of prominent native and Ponto-Caspian taxa across site groups suggested a highly species-specific response to *D. polymorpha*.

The clear, positive relationship of Ponto-Caspian amphipod *D. villosus* with *D. polymorpha* was notable in this respect. As discussed, comparable associations have been found for invasive Ponto-Caspian amphipods in the North American Great Lakes (Stewart et al. 1998; Bially and Mac Isaac 2000; Nalepa et al 2001) alongside European lentic and river systems (Gallardo and Aldridge 2015; Maresaux et al. 2016); however, the correlation of *D. villosus* and *D. polymorpha* density appeared particularly strong in Barton Broad. The Ponto-Caspian was not found at sites where *D. polymorpha* were absent and according to Spearman's Rank analysis, was more strongly correlated with *D. polymorpha* than any major taxa in the study. Dissimilarity in community composition between higher and lower density mussel sites was consistently driven most by *D. villosus* abundance. Further, *D. villosus* provided the only clearly structured (linear), positive relationship with *D. polymorpha* of any taxa in the study. Given otherwise homogenous conditions; this provided evidence for a particularly strong, species-specific relationship with *D. polymorpha* mussel beds in Barton Broad.

Like for aforementioned studies showing positive invertebrate correlations with *D. polymorpha*, a series of commensal mechanisms with *D. polymorpha* could explain the association with *D. villosus* in Barton Broad. Though not tested in this work, examples include food provision from byssus and pseudofacaes excretion (Stewart and Haynes 1994; MacIsaac

1996; Pace 1998) on which *D. villosus* have been shown to feed (Platvoet et al. 2009*b*). Also, the physical structure of mussel beds may provide complex interstices between shells that give cohabiting invertebrates refugia from flow (Ricciardi *et al*., 1997) and predation (González & Downing, 1999; Ward & Ricciardi 2007) alongside increased habitable surface area (Stewart et al. 1998*b*; Marescaux et al. 2015). It was notable that for the latter case, effects can be provided by dead *Dreissena* spp. shells (Botts et al. 1996; Horvath 1999). For the higher density *D. polymorpha* sites in Barton Broad, mean bed substrate composition was largely dead shells (69-77%), of which 90-94% were *D. polymorpha*. Given that soft silt sediments were the only other major substrate type across Barton Broad, the importance of such features could be particularly important for cohabiting *D. villosus*. These amphipods were not only strongly positively correlated with dead *D. polymorpha* shell density, but strongly negatively correlated with the weight of substrate silt component.

Considering this host of theoretically beneficial trophic and physical impacts of live and dead *Dreissena* spp. (*sensu* Stewart and Haynes 1998*b*); negative correlation of mussel density with two dominant native taxa was surprising. Firstly, Chironomidae spp. density, like for amphipods, has been widely shown to positively correlate with *Dreissena* spp. in the North American Great Lakes (Griffiths 1994; Ricciardi 1994; Stewart and Haynes 1994;) alongside European lentic and river systems (Lewandowski 1976; Karatayev et al. 1997). In particular, studies suggest Chironomidae spp. benefit from consumption of pseudofacaes excreted by live mussels (Griffiths 1993; Karatayev et al. 1997) and may be generally facilitated by refugia associated with increased substrate complexity from mussel shells (Ricciardi 1994; Botts et al., 1996). The fact we did not evidence a positive relationship of Chironomidae spp. with *D. polymorpha* did not adhere to a general facilitation model of mussel impacts in Barton Broad.

Likewise, Oligochaeta spp. presented a clear negative relationship with *D. polymorpha* despite positive associations shown in other lentic (e.g. Lewandowski 1976; Stewart and Haynes 1994;

Haynes et al. 2005) and lotic environments (Moroz 1994). Previously discussed trophic and physical benefits of mussel beds have been considered exploitable by this group (Armendáriz et al. 2011). In particular, the importance of flow refugia has been suggested for Oligochaeta spp., albeit in stream studies (e.g. Rempel et al. 1999; Syrovátka et al. 2009). Given this, we considered whether specific environmental factors of our study site influenced findings. For example, Oligochaeta spp., most notably the common subgroup Tubificidae spp., are a predominantly burrowing taxon. Oligochaetes process soft sediment for food resources (Tevesz et al. 1980; Mermillod-Blondin et al. 2001) and utilise the hyporheic as refugia for adult (Fisher and Beeton 1975; Milbrink 1973) and cocoon life stages (Newrkla and Mutayoba 1987). It was possible that at study sites where bed substrate was dominated by *D. polymorpha* shells, Oligochaeta were not provided with such advantages. Deleterious anoxia may also be more prevalent in sediments underlying mussel beds; suggested to explain decline of burrowing amphipod *Diporeia* spp. in the North American Great Lakes region (Ward and Ricciardi 2007) and polychaete *Marphysa depressa* in a South African lagoon (but with Meditteranean mussel *Mytilus galloprovincialis*; Robinson & Griffiths 2002).

Explanation for the negative relationship of Chironomidae spp. with *D. polymorpha* was less clear. However, it was possible cohabiting *D. villosus*, strongly associated with *D. polymorpha* beds, exerted deleterious predation pressure. Indeed, *D. villosus* have been shown as highly predacious on a variety of invertebrate taxa (Dick and Platvoet 2000; Dick and Platvoet 2002; MacNeil and Platvoet 2005), including Chironomidae spp. larvae in laboratory tests (Platvoet et al. 2009*b*). Though few studies have demonstrated impacts *in-situ*, this factor may have influenced the Chironomidae spp. distribution found. Alternatively, Chironomidae spp. populations on mussel beds may be more strongly pressured from benthivorous fish predation compared to *D. villosus*. For example, the striped pigmentation pattern of the *D. villosus* exoskeleton, similar to that of *D. polymorpha* shells could provide a competitive advantage

over Chrionomidae spp. due to camouflage effects (see: Magwick and Aldridge 2011; MacNeil et al. 2012). *D. villosus* have been shown to perform well under piscine feeding on mussel beds compared to native taxa (Kobak et al. 2014), possibly due to such co-evolved traits. Regardless, the disassociation of Chironomidae spp. with *D. polymorpha* beds appeared to disagree with a model of general facilitation by the mussel in Barton Broad. Further, if deleterious predation mechanisms for Chironomidae spp. on *D. polymorpha* mussel beds were proven, it would provide evidence of clear Invasional Meltdown mechanisms in Barton Broad.

Similar interactions could help explain the distribution of another important native species in this study, the gastropod *V. viviparus*, which was positively associated with both live *D. polymopha* and empty shells. For example, comparatively robust taxa would be expected to predominate at sites of high *D. polymorpha* density if greater rates of benthos predation occurred there (i.e. from *Dikerogammarus* spp.). With a relatively large size and robust shell, even at juvenile life stages (Keller and Ribi 1992); *Viviparus* spp. could clearly be less liable than Chironomidae spp. to predation. Indeed, *Viviparus* spp. have shown greater resistance to piscine feeding compared to other invertebrates (Ribi 1986) and would be more unlikely to face such pressures from amphipod *D. villosus* than Chrionomidae spp.. Further, *V. viviparus* may also benefit from trophic and physical benefits of *D. polymorpha* already discussed. In particular, scraper-feeding gastropods such as *V. viviparus* have been positively associated with the provision of biofilm food sources on *D. polymorpha* shells (Ward and Ricciardi 2007; Ricciardi et al. 1997). Again, regardless of the mechanisms involved, our results clearly supported a model of species-specific, rather than general facilitation by *D. polymorpha*.

The strong, positive association of Ponto-Caspian amphipods to *D. polymorpha*, notably *D. villosus*, was also broadly supportive of an Invasional Meltdown model. As one of the few UK studies to quantitively assess species associations with *D. polymorpha in situ*; we can highlight Barton Broad as a site where facilitation between Ponto-Caspian invasives is clearly evidenced

and distribution of certain native taxa does not appear to indicate expected, comparable benefits from *Dreissena* spp.. Similar observations have been used elsewhere to demonstrate evidence for potential invasional meltdown processes (e.g. Ricciardi 2001; Marescaux et al. 2016); though it should be stressed, analogous community responses to mussel beds may not be applicabile elsewhere due to specific environmental aspects of the study site.

Notably, the influence of *D. polymorpha* in Barton Broad may be greater than for other environments because live and dead shells provided the only source of hard substrate present. In this case, *D. polymorpha* gave comparatively distinct niche opportunities (see: Hutchinson 1978) for invertebrate communities; which may have resulted in more strongly segregated species distribution. For example, if *D. villosus* were largely facilitated by the provision of hard bed interstices; similar impacts to mussel shells could be achieved by mineral pebble or cobble substrates where such features were more common. Likewise, lower densities of major burrowing taxa such as Oligochaeta spp. would be naturally expected throughout sites with predominantly hard substrate composition (See: Ladle and Bird 1980; McElhone 1982; Syrovátka et al. 2009; Extence et al. 2011), regardless of mussel density. Distinct trends found for benthic communities at Barton Broad would be less likely to occur in these cases. Exemplary environments could include high order lotic sites or mountain lakes with limited fine sediment flux. Such differences may have driven conflicting observations of invertebrate response to *D. polymorpha* (e.g. general facilitation, species specific facilitation, IMH) in previous field studies.

Future research could aim to assess which types of invaded environments are more liable to community structuring by *Dreissena* spp. when compared to others. In particular, isolating conditions where strong commensal relationships with other Ponto-Caspians are most likely to develop would be of value. This study clearly shows an affinity of high concern Ponto-Caspian species to *Dreissena* spp. mussel beds, presenting a benchmark for species associations for at

least one environment type. Considering recent arrival of a new Dreissenid *D. r. bugensis* to the UK, work to elucidate where similar impacts may occur would be particularly timely. Over long-time scales *D. r. bugensis* have replaced *D. polymorpha* in cohabited invaded environments (Haynes et al. 2005; Marescaux et al. 2015) and while the UK range of *D. r. bugensis* is currently restricted, it will likely to expand (Aldridge 2014). Increased risk of invasional meltdown processes, in at least some environments, would then be expected.

Conclusions

Benthic invertebrate communities in Barton Broad were strongly influenced by *D. polymorpha*. Distinct variations in community composition were identified among sites categorised by different mussel densities. Similar to findings of other studies, invertebrate richness and density was greater where *D. polymorpha* was more abundant and bed substrate increasingly dominated by *D. polymorpha* shells. The otherwise homogenous physicochemical nature of Barton Broad suggested main factors driving community differences between site groups were the presence of live and dead *D. polymorpha* or the amount of substrate composed of silt.

Despite overall positive trends for invertebrate richness and density, clear segregation of prominent native and Ponto-Caspian taxa across site groups suggested highly specific species responses to *D. polymorpha*. For example, Ponto-Caspian amphipods *D. villosus* and *C. curvispinum* were positively associated with both live and dead *D. polymorpha*, alongside native gastropod *V. viviparis*. Relationships of these taxa with *D. polymorpha* strongly contrasted with the negative associations of prominent native groups Chironomidae spp. and Oligochaeta spp; which in turn were positively associated with increasing silt substrate composition.

The negative relationship of Oligochaeta spp. with both live and dead *D. polymropha* may have been driven by mussel shell material acting as an unfavourable, hard substrate component at

high density mussel sites. For example, as a predominantly burrowing taxa group, Oligochaeta were shown in other studies to negatively respond to hard substrate environments, including mussel beds specifically. Across sites, Oligochaeta spp. were also more strongly positively associated with increasing silt substrate component compared to any taxa.

For Chironomidae spp., facilitative impacts from *D. polymorpha* were certainly expected but not identified in this study. We speculated that high *D. villosus* density on mussel beds could drive reduced cohabiting Chrironomidae spp. due to predatory interaction. Alternatively, benthivorous fish may have preferentially consumed Chironomids on mussel beds due to more effective *D. villosus* performance under similar predation pressure. Regardless of mechanism, our results clearly supported a model of species-specific, rather than general facilitation by *D. polymorpha* in Barton Broad. We noted the native gastropod *V. viviparus* was likely more robust to predation than Chironomidae spp.; perhaps contributing to a comparably positive association with mussel beds in Barton Broad.

The risk of *Dreissena* spp. acting as a pioneer species under IMH appears to be underlined by this study. Not least, this may be relevant considering the arrival of a new invasive *Dreissena* species in the UK, *D. r. bugensis*. However, further extrapolation of our findings remain problematic. The influence of *Dreissena* spp. in structuring invertebrate communities may be greater in Barton Broad than for other environments. Mussel beds appeared to form a particularly distinct habitat compared to a relatively homogenous surrounding benthic environment. Future research could aim to examine which types of environments invaded by *D. polymorpha* are at greater risk of community structuring by *Dreissena* spp. compared to others, including facilitation of other invasive species. Studies could assess which types of invaded environments were most liable to community structuring by *Dreissena* spp.. In particular, isolating conditions where strong commensal relationships with other Ponto-Caspians were more likely to develop would be of value.

Part 3: Likelihood of Impact

Assessing the probability of significant impacts of D. r. bugensis in invaded UK freshwater environments.

Chapter 7 – *Physical factors influencing D. r. bugensis density and population distribution in the Wraysbury River UK; 4 years after first record.*

Summary:

When established in a new geographic region, the success and ecological impacts of a non-native species may vary compared to environments elsewhere. Considering the recent arrival of the invasive bivalve mollusc *Dreissena rostriformis bugensis* to UK freshwaters, this study aimed to provide a timely assessment of *D. r. bugensis* habitat preferences within the known invaded range. Four years after the first UK record (September 2018); an intensive, systematic survey of mussel populations in the Wraysbury River, Surrey, was undertaken. *D. r. bugensis* associations with a series of physical stream parameters were tested through correlation and regression techniques across a series of environmentally variable study sites. Based on previous literature findings, selected parameters included stream depth, longitudinal velocity, solar exposure and bed substrate composition as % boulder, % cobble, % pebble, %gravel, %sand or %silt size classes. A final parameter was sample distance from the *D. r. bugensis* upstream limit; located at the reservoir outlet pipe in previous study (**Chapter 2**; 30 pp.).

In general, *D. r. bugensis* appeared to be well established throughout the ~2km^{-1} study reach with markedly increased population densities compared to previous surveys documented in this dissertation (e.g. **Chapter 2**; 2015-16). Notably, mussels were most clearly associated with downstream distance from the known upstream limit alongside the factor of stream depth; complimenting studies in similar invaded environments elsewhere. However, for several stream parameters, expected relationships were not found and *D. r. bugensis* in Wraysbury River had readily established across a wider range of physical conditions than might be expected from previous study. It was suggested the species could feasibly spread to a variety of similar regional settings and that populations in the known invaded reach were increasing. Both findings were of interest considering results of other chapters in this dissertation; whereby a holistic variety of *D. r. bugensis* impacts appeared driven by the factor of mussel density. Results may assist the prediction of potential spread and subsequent impact within this area and similar regional settings. This chapter provides a bridge to the overall project conclusions.

Introduction

Following establishment, the success of novel invasive species may vary across environmental conditions in the recipient region (Peterson 2003; Jiménez-Valverde et al. 2011). A series of physicochemical and biological environmental factors can determine distribution and density of alien taxa (Crooks et al. 1999; Peterson 2003). Knowledge of a species' preferred habitat assists prediction of future invasion pathways and species density across space (Peterson 2003; Kulhanek et al. 2011*a*). This is of importance because the density of a given species is likely to correlate with impacts on cohabiting ecology (Ricciardi 2003; Kulhanek et al. 2011*b*). Understanding potential invasive species densities in a recipient region may assist prediction of future impact magnitude. Accurate future impact scenarios are important to authorities in determining resource allocation for management (Byers et al. 2002).

Given knowledge of the preferred habitat of an invasive species; invasion risk assessment has been undertaken across large geographic regions according to environmental conditions present (Carlton 1996; Ricciardi and Rasmussen 1997). Examples for terrestrial environments include for plants (Meekins and McCarthy 2001; Ebeling et al. 2008), mammals (Peterson et al. 2006; Shiels et al. 2013), birds (Peterson et al. 2003; Strubbe et al. 2013) and insects (Adriaens et al. 2008; Meyer et al. 2010). For freshwater environments, macrophytes (Jacobs and MacIsaac 2009; Thum and Lennon 2010), invertebrates (Ricciardi 2003; Palaoro et al. 2013), reptiles (Rodda et al. 2009; Bisrat et al. 2012) and fish (Chen et al. 2007; Kulhanek 2011*b*). In aquatic and terrestrial environments, predictions may be complimented by contributions from expert knowledge (e.g. Roy et al. 2014; Wittmann et al. 2014). However, for some invasive species, limited invasion histories in environments comparable to that threatened can cause difficulty in the prediction of distribution and impacts (Kulhanek et al. 2011*b*).

The establishment of the 'quagga mussel' *Dreissena rostriformis bugensis* (Andrusov 1897) in the UK may be challenging in this respect. An epifaunal bivalve mollusc, *D. r. bugensis* has established invasive populations across varied regions outside a native range of the Ukrainian Ponto-Caspian region (Ricciardi and Rasmussen 1995). For example, when first recorded in North America at Great Lake St. Ontario in 1991 (May and Marsden 1992), *D. r. bugensis* achieved an extensive spatial range between Lake Erie and the city of Quebec (~1100km^{-1} apart) within 2 years (Mills et al. 1993*b*). At later points, researchers reported mussel densities of 16,400 m^{-2} for Lake Michigan (Nalepa et al. 2009), 75,300 m^{-2} in Lake Huron (Nalepa et al. 1995), 342,000 m^{-2} in Lake Erie (Howell et al. 1996), 17,000 m^{-2} in the Hudson River (Strayer et al. 1996), and 11,400 m^{-2} in the upper Mississippi River (Cope et al. 1997). This comparatively recent, late 20th Century invasion contributed to a wealth of studies from North America where impacts of *Dreissena* spp. on cohabiting ecology were identified (Strayer et al. 1999; Vanderploeg et ak, 2002; Strayer 2010) with their magnitude correlated with mussel density (Ward and Ricciardi 2007).

While invasive *D. r. bugensis* populations have also been recorded in European river and canal networks in Russia (Orlova et al. 2004), Poland (Soroka 2002), Germany (Velde and Platvoet 2007), France (Bij de Vaate and Beisel 2011l Marescaux et al. 2012) the Netherlands (Bij de Vaate 2010; Matthews et al. 2014) and lentic systems across eastern Europe (Karatayev et al. 2015); the majority of quantitative of studies on *D. r. bugensis* distribution have been undertaken in the North American Great Lakes and associated, deep river systems (Jones and Ricciardi 2005). Resultingly, information on the ecological niche and preferred habitat of invasive *Dreissena* spp. has been derived predominantly from North American studies.

The environmental parameters tested to explain species distribution should be guided by known traits of the organism (Peterson and Nakazawa 2008). However, environments invaded by *D. r. bugensis* in the UK contrast significantly from those of the North American Great Lakes. For

example, the only known site recording mussel densities higher than >5 individuals m^{-2} has been the Wraysbury River, Surrey. As discussed elsewhere in this project, a small (< 5m width, $0.5m^{-1}$), shallow tributary of the River Thames. Notably, self-sustaining populations of *Dreissena* spp. have not been considered likely to establish in such environments (Hovarth et al. 1996; Lucy et al. 2008). In small rivers, there remains little understanding of the preferred habitat of *D. r. bugensis* and what densities *D. r. bugensis* populations may potentially attain.

Despite limited work in comparable environments, variation of *D. r. bugensis* density in Wraysbury River was expected to be broadly associated with certain physical conditions. Firstly, *D. r. bugensis* has been shown to favour solid substrate size classes such as boulders, cobbles and artificial banking (Mellina and Rasmussen 1994; Strayer et al. 1996; Karatayev et al. 1998). Also, in less illuminated, deep water; vulnerability of *Dreissena* spp. to visual predation by waterfowl and fish may be reduced (Karatayev et al., 1997; Petrie & Knapton, 1999; Haynes et al., 1999) with enhanced survival rates of early-stage larval veligers from lower ultraviolet radiation exposure (Seaver et al. 2009; Thaw et al., 2014). Further, reduced stream flow velocities (<0.2 m s^{-1}) have been shown favourable to mussel feeding (Ackerman 1999) and *Dreissena* spp. have generally been found at highest densities in still, lentic systems (Ramcharan et al. 1992; Aldridge 2014). As such, it was hypothesised that where bed substrate (i) contained a higher proportion of larger substrate size classes, (ii) was subject to increased water depth, (iii) reduced solar exposure and (iv) lower flow velocities: higher densities of *D. r. bugensis* would be found in the known UK range.

The primary aim of this chapter was to assess the preferred habitats of *D. r. bugensis* in the Wraysbury River. By quantitively surveying mussel distribution across various in-stream habitats; the objective was to elucidate which environmental conditions were associated with the highest *D. r. bugensis* densities at this site. It was hoped that knowledge of *D. r. bugensis* distribution trends would facilitate analysis of future establishment risk and subsequent

ecological impacts within similar regional settings. In this respect, this chapter provides a bridge to the overall project conclusions and synthesis which follow (**Chapter 8**; 203 pp.).

Methodology

Study Area

Between 21st May and 4th June 2018 an intensive, systematic survey of *D. r. bugensis* populations in the Wraysbury River was conducted in Surrey, UK. Work was undertaken throughout a 1.8 km^{-1} study reach within the known range of *D. r. bugensis*. Previous study had shown this section of the river was a small (<5m^{-1} wide), shallow (<0.5m^{-1} depth) stream with predominantly gravel-pebble substrate and glide flow characteristics (See **Chapter 2** and **Chapter 3**; 30 pp. and 57 pp., respectively). For this study we more closely interrogated these conditions and included downstream sites not previously visited. In total, we surveyed 10 sampling sites grouped as 'upstream', 'midstream' and 'downstream' sections of the study reach for descriptive purpose (**Figure 7.1**). All sites surveyed for **Chapter 2** in 2016, within the invaded *D. r. bugensis* range (see: **Figure 2.1** pp.) were included in this study alongside 4 new sites (numbers 4, 5, 8 & 10 in this study; **Figure 7.1**).

Surrounding land uses included pastoral moorland and a section of the London orbital motorway (M25) in the upstream and midstream site groups (Sites 1-2 and 3-6, respectively); with deciduous woodland and disused canals characterising the downstream sections (sites 7 to 10). Seasonal stream chemistry records collected by the UK Environment Agency between May 2017 and May 2018 gave mean nutrient concentrations for the Wraysbury River as total Nitrate 8.6 N mg L^{-1} and orthophosphate 0.24 mg L^{-1} with stream alkalinity 220 mg L^{-1} as CaCO3 (EA, pers. com. 2018; **Appendix IV**, 274 pp.). Previous study between 2015-16 had

determined mean *D. r. bugensis* densities of 54 individuals m^{-2} in the Wraysbury River with the largest populations found in upstream sections of the reach (Mills et al. 2017).

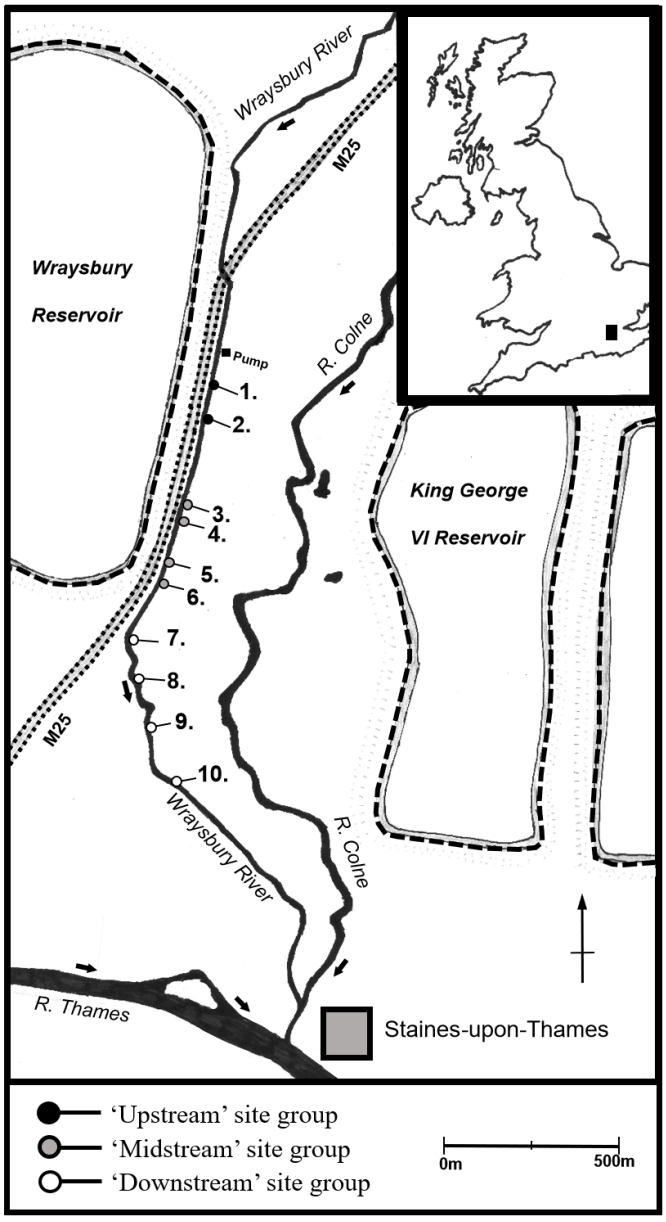


Figure 7.1 Map showing study reach and study site location (Lat 51.45225; Long -0.520528). As study site groups; Sites 1 and 2 are denoted as 'upstream,' 3-6 'midstream' and 7-10 'downstream.' The location of the reservoir pump facility is also noted; thought to be the upstream limit of *D. r. bugensis* in the Wraysbury River (Lat 51.457730; Long -0.518159).

Data Collection

Mussel densities were sampled randomly at each of the 10 study sites and paired with corresponding stream physical measurements at the exact point of mussel sampling. Study sites were standardised in size to a length of one bank width; measured with a tape measure and delineated with ranging poles. Per site, a grid system of 5 x 5 equidistant points within the sampling area was used to randomly determine sampling location for *D. r. bugensis* density and paired physicochemical parameters. Using a random number generator, 10 sampling points per-site were selected, according to randomised *x* and *y* coordinates on the grid.

At each sampling point 10 stream physical variables were measured. Stream depth was recorded to the nearest cm^{-1} with a ranging pole and longitudinal flow velocity at 0.6 depth was measured using a Valeport electromagnetic flow meter (model 801) operating with a 30 second-average velocity function. Stream pH, dissolved oxygen (DO; mg L^{-1}), conductivity (µs cm^{-1}) and temperature (^{o}C) were also recorded using a HACH™ HQ30d multi-probe and HI9811-5N pH/EC/TDS/°C portable meter.

To indicate stream solar exposure, midday light intensity (LUX) was measured at the water surface above each sampling point with a series of 6 measurements using a SODIAL LX1330B light meter. At initial visits for two sites (9 & 10; fieldwork conducted on May 31st and June 1st, respectively); light measurements could not be undertaken because weather conditions were overcast and incomparable to clear weather measures made on different days at other sites. Sampling points at these missed locations were revisited on June 3rd to take solar exposure measurements when weather conditions were clear.

Following assessment of stream depth, flow and light exposure, benthic substrate was collected at each sampling point using a surber sampler (0.33 x 0.33m; net mesh size 250 μm^{-1}) placed on the stream bed. In each case, bed substrate was excavated to a depth of $2cm^{-1}$ within the

surber sampler frame using a trowel. Contents were displaced into the surber sampler netting for transport to the bankside and further processing. When emptied into a sorting tray, sample contents were examined closely for live *D. r. bugensis* specimens which were enumerated and separated from the remaining benthic sample.

For each of 10 benthic samples per study site, materials were passed through field sieves to isolate components corresponding to different substrate size classes. As per the Wentworth Scale (See: Wentworth 1922); Boulders, cobbles, pebbles, gravels and fines were separated by mesh sizes of $256mm^{-2}$, $64mm^{-2}$, $4mm^{-2}$, $2mm^{-2}$ respectively. Except for fines, classed components were left to dry on the bank side for a period of approximately 2 hours before being individually weighed using portable field scales (model). The fines collected per sample were stored in labelled polyethene bags for transport to the laboratory. Oven drying was conducted on samples at 400^{o}C for 5 hours before separation and weighing. Sand components were separated from silts using a 355 μm^{-2} mesh sieve and individually weighed using a high sensitivity balance (model). Using total weights for each size class per sample, we calculated the percentage contribution of cobble, coarse pebble, fine pebble, gravel, sand and silt to total substrate composition.

The 9 stream physical parameters used in analysis of *D. r. bugensis* habiat preferences included [1]stream depth (m^{-1}), [2]longitudinal velocity ($m\ s^{-1}$), [3]solar exposure (Lux), substrate proportion as [4]% boulder, [5]% cobble, [6]% pebble, [7]%gravel, [8]%sand, and [9]%silt size classes. A final parameter included was site [10]distance (km^{-1}) from the *D. r. bugensis* upstream limit; with an assumed location at the reservoir outlet pipe in previous study (explained **Chapter 2**; 30 pp.). This parameter was added because the upstream proximity of longer established or more highly reproductive adult populations for larval veligers has been regarded important for *Dreissena* spp. distribution in rivers of the North American Great Lakes region (Hovarth and Lamberti 1999; Stoeckel et al. 1997) and River Don and Volga basins of Russia (Zhulidov et al. 2005).

All sample points within sites were given the same site-specific value calculated through pathway functions on Google Earth Pro^{TM} software (Version: 7.3.1.4507; 2018).

Analysis

To summarise *D. r. bugensis* densities throughout the study reach, we firstly plotted mean density (individuals m^{-2}) with distance downstream the study reach (km^{-1}). For comparative purpose, mean *D. r. bugensis* density data from annual 2015-16 surveys (See: **Chapter 2**; **Figure 2.2**; 40 pp.) were also shown. Stream physical parameters were then summarised and variation between site averages was tested to confirm a range of different environmental conditions were found in the study reach. We conducted a series of ANOVAs between sites comparing stream depth (cm^{-1}), velocity ($m\ s^{-1}$), solar exposure (Lux) and the percent substrate contributions of boulder, cobble, pebble, gravel, sand and silt clast sizes, respectively. Data failed to meet parametric assumptions even after transformations for stream longitudinal velocity ($m\ s^{-1}$), solar exposure (Lux) and percentage substrate contribution of gravel, sand and silt clasts. In these cases, we used ANOVA on ranks instead. For all parameters, where there was significant variation between study sites we used Tukey's *post hoc* multiple comparison tests to elucidate site differences. To further explore variation in stream physical characteristics across study sites; data from all sampling points was also summarized with principal components analysis (PCA); incorporating all 10 physical stream parameters. We plotted eigenvalue coordinates for PC1 and PC2 with sampling points labelled by site number and symbols denoting 'upstream,' 'midstream' and 'downstream' study site categories. A loadings plot was used to demonstrate stream physical variables influential for PC1 and PC2 coordinate scores. All analysis was undertaken using Sigmaplot 13.0 (Systat Software, Chicago, Illinois, USA).

Forward-stepwise multiple linear regression was used to select the best model for predicting *D. r. bugensis* density across all sites (p=0.05 to enter the model). For independent variables, all stream physical parameters were included; these being [1]stream depth (m^{-1}), [2]longitudinal velocity (m s^{-1}), [3]solar exposure (Lux), substrate proportion as [4]% boulder, [5]% cobble, [6]% pebble, [7]%gravel, [8]%sand, and [9]%silt size classes alongside site [10]distance (km^{-1}) from the *D. r. bugensis* upstream limit. Where independent variables were significant in the prediction of *D. r. bugensis* densities, simple linear regression was performed, if appropriate, to assess how much variability in *D. r. bugensis* across sites could be explained for individual parameters. Prior to analysis, the residuals of physical parameters for all regression models were assessed for normality and homoscedasticity. Data for (i) *D. r. bugensis* density (individuals m^{-2}) and (ii) site distance from upstream *D. r. bugensis* limit (km^{-1}) were log (n +1) and log transformed, respectively, to better fit model assumptions.

Forward stepwise multiple regression was then conducted within 'upstream', 'midstream' and 'downstream' study site groups (See: **Figure 7.1**); again, to find the best model for predicting *D. r. bugensis* density according to all physical stream parameters (but excluding distance from upstream *D. r. bugensis* limit (km^{-1})). By testing within site groups, the objective was to identify environmental trends in *D. r. bugensis* distribution that excluded confoundment from site distance from the upstream limit of *D. r. bugensis*. Again, prior to analysis the residuals of physical parameters for all regression models were assessed for normality and homoscedasticity. Data for (i) *D. r. bugensis* density (individuals m^{-2}) were log (n + 1) transformed to better fit model assumptions. All analysis was undertaken using Sigmaplot 13.0 (Systat Software, Chicago, Illinois, USA).

Results

Upstream study sites presented higher *D. r. bugensis* denisity (individuals m^{-2}) in comparison to those downstream with clear decline through the study reach. According to ANOVA on ranks, strongly significant between-site variation in *D. r. bugensis* density (individuals m^{-2}) was found (p = <0.001) and appeared driven by values at the four highest density sites (i.e. 1, 2, 4 & 5) when compared to the two most downstream (i.e. 9 & 10), low density sites (**Table 7.1**). Mean densities of *D. r. bugensis* across the study reach were (122 individuals m^{-2}); 56% higher than found for our 2015-16 studies (54 individuals m^{-2}; see: Mills et al. 2017). Throughout the reach, mean *D. r. bugensis* densities appeared consistently higher than found in 2015-16; though similarly appeared to decrease with downstream distance through the catchment before becoming negligible at approximately 1.4km^{-1} from the upstream *D. r. bugensis* limit (**Figure 7.2**).

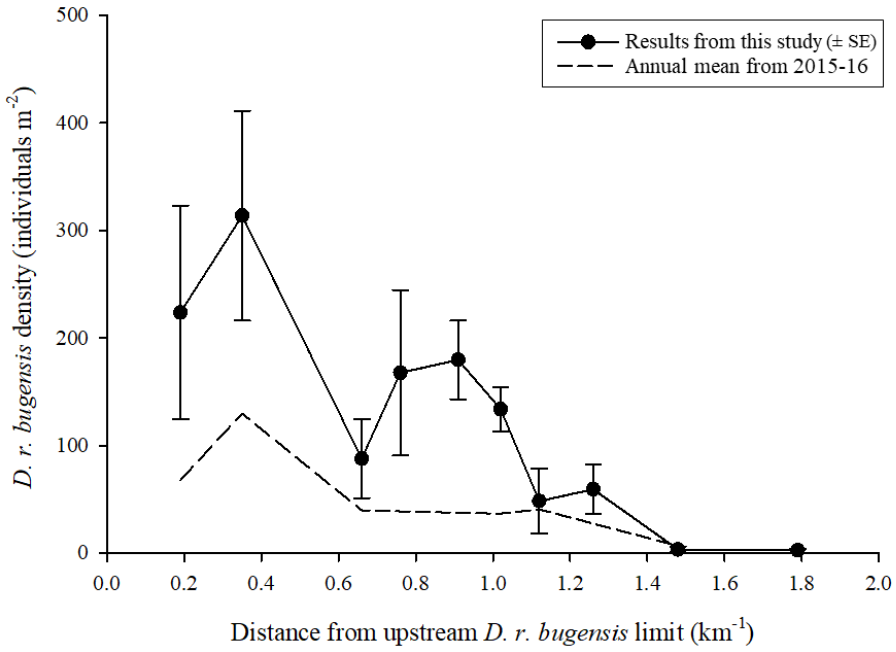


Figure 7.2 Mean *D. r. bugensis* density (individuals m^{-2}) with distance from upstream *D. r. bugensis* limit (km^{-1}). Filled line denote results from this study (± SE) with dotted line showing annual mean recorded in 2015-16 survey (see: Mills et al. 2017).

Stream physical parameters also presented varied mean values between sites (**Table 7.1**). According to ANOVA, the only measures not significantly different were stream longitudinal

velocity (range: 0.15-0.17 m s^{-1}) and % cobble in total substrate composition (range: 16 - 32 %). Alternatively, stream depth (range: 0.27 – 0.55 m^{-1}) was strongly significantly different between sites according to ANOVA (p = <0.001), driven by higher values at sites 8 and 2 alongside lower values at the most downstream site. Stream solar exposure (range: 30 – 870 Lux) also varied significantly between sites (p = 0.001) driven by higher values at a series of midstream and downstream sites (i.e. 10, 9, 8, 6, 5) in comparison two midstream sites (i.e. 3 and 4).

For stream physical parameters related to bed substrate; all clast size classes except cobbles presented significantly different percentages of total substrate composition between sites (**Table 7.1**). Sand and Silt categories (range: 13 - 41%, 2.8 - 29%, respectively) were both strongly significantly different between sites according to ANOVA (p = <0.001); largely driven by lower values at the second most downstream site (i.e. 9). The gravel category (range: 1.0 – 9%) also presented strong significant differences between sites (p = <0.001), which appeared driven by higher values at one midstream site (i.e. 7). Finally, the pebble category (range: 17 – 35%) showed moderate differences between sites (p = 0.002), driven by high values at the most upstream site.

Principal components analysis (PCA) showed PC1 and PC2 accounted for 42% of the variance of stream physical parameters in the study (**Figure 7.3**). Across the sampling points the scoring plot for PC1 and PC2 suggested site grouping accordant to stream physical parameters. The most upstream study sites appeared to be clustered away from the most downstream sites with those in the midstream scattered between (**Figure 7.3a**). Examining the loadings plot (**Figure 7.3b**), more downstream sites were associated most with directional axes for ‘distance from the known *D. r. bugensis* limit (log km^{-1})’ and ‘stream solar exposure (lux)’. Upstream sites appeared more associated with increasing % of pebble and boulder clast contribution to substrate composition.

Table 7.1 Mean *D. r. bugensis* density (individuals m^{-2}) and stream physical parameters per site (± SE). Between-site results of ANOVA and *post hoc* Tukey's test for each variable also shown; except for the variable 'km^{-1} distance from upstream *D. r. bugensis* limit', where there was no variation within site values.

Study Site	*D. r. bugensis* density (m^{-2})	Stream depth (m^{-1})	*x* Velocity ($m\,s^{-1}$)	Midday Solar Exposure (lux)	% Cobble Substrate	% Pebble Substrate	% Gravel Substrate	% Sand Substrate	% Silt Substrate	km^{-1} fr. *D.r.bugensis* upstream limit
1	224 ± 99	37.3 ± 2.5	0.24 ± 0.02	318 ± 138	32 ± 3.9	35 ± 2.2	4.4 ± 0.9	15.7 ± 4.2	2.8 ± 1.3	0.19
2	314 ± 98	41.9 ± 1.9	0.24 ± 0.04	275 ± 104	28 ± 4.5	32 ± 3.1	4.2 ± 0.8	25.0 ± 3.1	9.2 ± 3.1	0.35
3	88 ± 37	33.6 ± 1.8	0.20 ± 0.03	30 ± 6	33 ± 3.7	18 ± 3	1.0 ± 0.3	19.2 ± 2.2	20.8 ± 2.2	0.66
4	168 ± 77	41.5 ± 1.7	0.15 ± 0.02	49 ± 19	21 ± 4.1	31 ± 3	1.6 ± 0.4	20.4 ± 1.7	26.3 ± 1.4	0.76
5	180 ± 37	37.4 ± 1.5	0.31 ± 0.03	841 ± 143	32 ± 6.2	22 ± 4	5.6 ± 1.7	30.8 ± 3.7	9.0 ± 1.7	0.91
6	134 ± 21	38.3 ± 1.1	0.21 ± 0.02	681 ± 84	32 ± 6.3	17 ± 5	4.9 ± 1.0	16.3 ± 4.3	28.8 ± 4.9	1.02
7	49 ± 30	37.6 ± 1.6	0.27 ± 0.05	483 ± 105	24 ± 9	20 ± 2	9.0 ± 2.1	32.3 ± 5.5	11.7 ± 2.3	1.12
8	60 ± 23	54.9 ± 1.6	0.23 ± 0.04	870 ± 86	16 ± 6	24 ± 4	2.1 ± 1.0	41.0 ± 3.1	17.3 ± 2.4	1.26
9	4 ± 3	40.7 ± 1.9	0.27 ± 0.04	683 ± 121	43 ± 6	29 ± 3	3.5 ± 0.6	12.8 ± 1.8	6.8 ± 3.5	1.48
10	3 ± 2	26.9 ± 1.7	0.19 ± 0.05	787 ± 97	25 ± 7	30 ± 4	3.9 ± 1.3	24.1 ± 3.4	15.4 ± 3.8	1.79
Test	$H = 48.8_{(9)}$	$F_{(9, 90)} = 3.8$	$H = 14.0_{(9)}$	$H = 14.0_{(9)}$	$F_{(9, 90)} = 3.8$	$F_{(9, 90)} = 3.3$	$H = 31.7_{(9)}$	$H = 40.0_{(9)}$	$H = 50.2_{(9)}$	n/a
***p* value**	**<0.001*****	**<0.001*****	0.124	**<0.001*****	0.102	**0.002***	**<0.001*****	**<0.001*****	**<0.001*****	
Tukey	2, 5 > 9, 10 6, 1 > 9, 10	8 > all, 2 > 3 10 < all expt 3	n/a	10, 9, 8 > 4, 3 6, 5 > 4, 3	n/a	1 > 6, 3	7 > 3, 8, 4	8 > 9, 1, 6, 5 > 9; 7 > 9	4, 8, 6 > 1; 6 > 9; 3 > 9	n/a

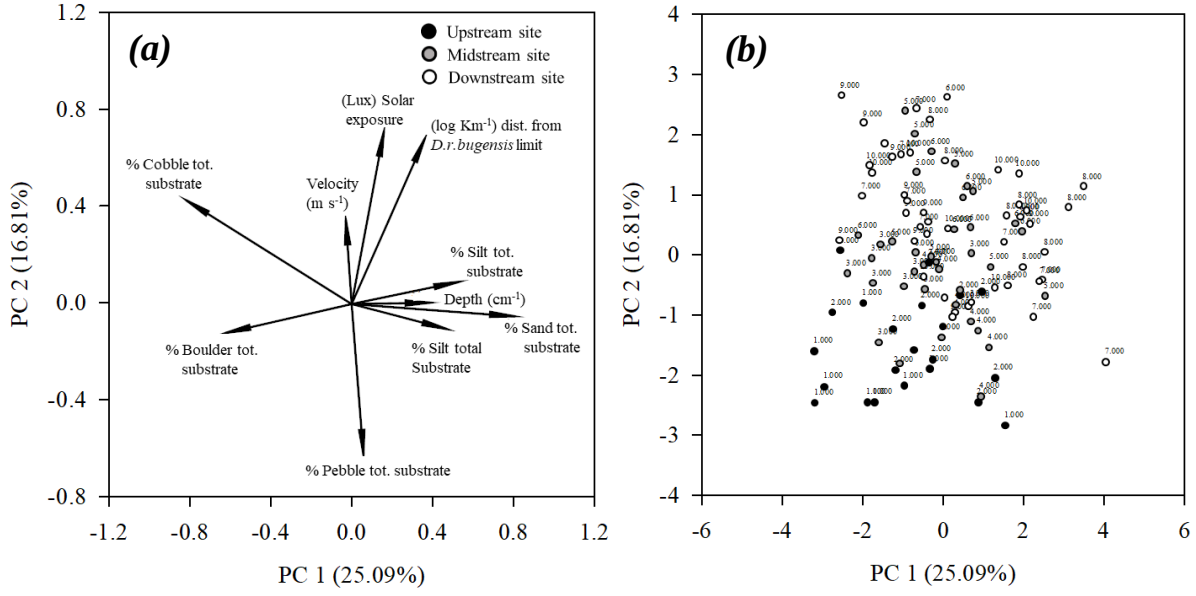


Figure 7.3 (*a*) Variation of stream physical parameters among sites summarized in principal components analysis (PCA) loading plot (PC1 and PC2) for the 10 variables. Stream physical parameters are represented by lines that point in the direction of influence. (*b*) Distribution of data scores across sampling locations on PC1 and PC2 coordinates with site number labels and plot symbols denoting upstream (blank circle), midstream (grey circle) and downstream (filled circle).

Forward stepwise multiple regression incorporating all 10 stream physical variables selected stream depth (cm^{-1}) and distance from *D. r. bugensis* upstream limit (Log km^{-1}) for predicting *D. r. bugensis* density (Log + 1 individuals m^{-2}) across all sites (based on p = <0.05). According to the model's R^2 value; 32% of variance in *D. r. bugensis* density was explained by these factors. Distance from the upstream *D. r. bugensis* limit (Log km^{-1}) showed strongly significant (p = <0.001), negative correlation and stream depth (cm^{-1}) moderately significant (p = 0.008) positive correlation with *D. r. bugensis* density (Log + 1 individuals m^{-2}; **Table 7.2**).

Simple linear regression plots presented variability in *D. r. bugensis* density (Log + 1 individuals m^{-2}) with distance from the known upstream limit (km^{-1}) across the study reach. The sample point distance from the upstream *D. r. bugensis* limit (Log km^{-1}) was clearly negatively correlated with *D. r. bugensis* density (**Figure 7.4***a*), explaining 27% of variability with high statistical significance (p = <0.001). Alternatively, stream depth was positively correlated with *D. r. bugensis* density, with a weak but significant relationship (p = 0.048) explaining 6% of variability (**Figure 7.4*b*)**.

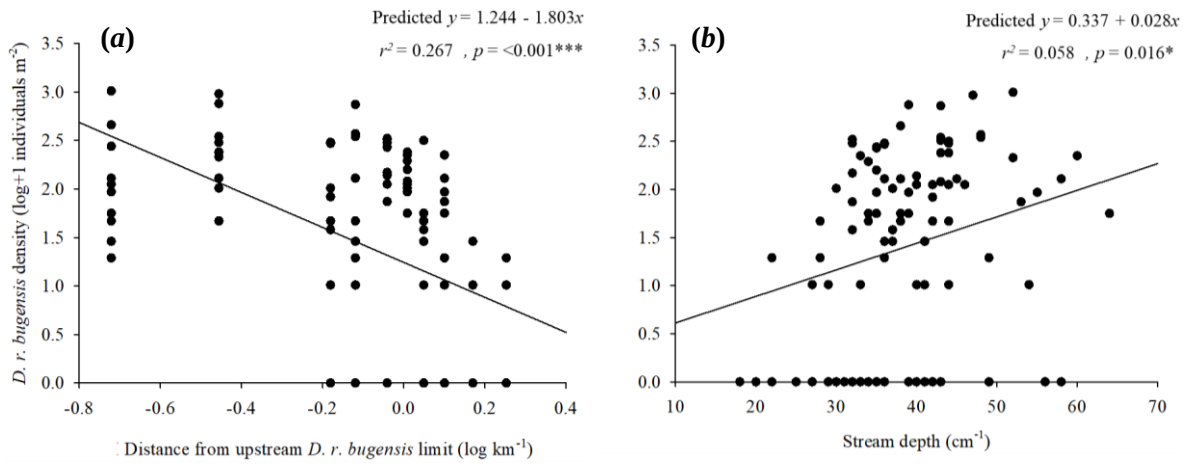


Figure 7.4 Regressions showing (*a*) *D. r. bugensis* density (log + 1 individuals m^{-2}) on distance from upstream *D. r. bugensis* limit (log km^{-1}) and (*b*) *D. r. bugensis density* (log + 1 individuals m^{-2}) on stream depth (cm^{-1})

Within upstream, midstream and downstream site groups, forward stepwise multiple regression incorporating all physical variables (excluding distance from known upstream limit) showed *D. r. bugensis* density was explained by a greater variety of factors than when tested across the whole reach. Within the upstream site group, analysis selected stream depth (cm^{-1}) and % cobble substrate composition for predicting *D. r. bugensis* density (Log + 1 individuals m^{-2}; **Table 7.2**). According to the model's R^2 value; 56% of variance in *D. r. bugensis* density was explained by these variables. Stream depth showed strong, significant (p = <0.001), positive correlation and percent cobble substrate composition showed moderately significant (p = 0.008) positive correlation.

For the midstream site group, forward stepwise multiple regression selected only stream longitudinal velocity (m s^{-1}) for predicting *D. r. bugensis* density (Log + 1 individuals m^{-2}). According to the model's R^2 value; 20% of variance in *D. r. bugensis* density was explained by this variable. Velocity showed weak but significant (p = 0.004), positive correlation with *D. r. bugensis* density (Log + 1 individuals m^{-2}; **Table 7.2**).

Similar analysis on the downstream site group selected stream depth (cm^{-1}) and % gravel substrate composition for predicting *D. r. bugensis* density (Log + 1 individuals m^{-2}). According to the model's R^2 value, 28% variance in *D. r. bugensis* density was explained by these variables. Stream depth showed moderately significant (p = 0.003), positive correlation and % gravel substrate composition, weakly significant (p = 0.024), positive correlation with *D. r. bugensis* density (Log + 1 individuals m^{-2}; **Table 7.2**; overleaf).

Table 7.2 Results of forward stepwise multiple regression of *D. r. bugensis* density (Log *n*+1; individuals m^{-2}) at (i) all sites and (ii) upstream, (iii) midstream (iv) downstream site groups on stream depth, longitudinal velocity, solar exposure and % boulder, cobble, pebble, gravel, sand or silt contribution to the bed substrate. Site distance from upstream limit of *D. r. bugensis* range used as an extra parameter in the 'all sites' test. Raw and standardized regression coefficients are given for the statistically significant physical variables.

Source	SS	df	MS	F	*p*	Regression Coefficients		R^2
						Raw	Std.	
All Sites *Log(n+1) D. r. bugensis density*:								
Regression model (all Sites)	30.833	2	15.416	22.696	<0.001***			0.319
– Log dist. from upstream *D. r. bugensis* limit (km^{-1})					<0.001***	-1.783	-0.511	
+ Stream Depth (cm)					0.008**	0.026	0.228	
Residual	65.887	97	0.679					
'Upstream' Site Group *Log (n+1) D. r. bugensis density*:								
Regression model (all Sites)	2.658	2	1.329	10.679	<0.001***			0.557
+ Stream depth (cm^{-1})					<0.001***	0.047	0.681	
+ % Cobble in total substrate composition					0.009**	0.187	0.488	
Residual	2.116	17	0.124					
'Midstream' Site Group *Log (n+1) D. r. bugensis density*:								
Regression Model (all Sites)	4.985	1	4.985	9.296	0.004**			0.197
+ Stream longitudinal velocity ($m\ s^{-1}$)					0.004**	3.706	0.443	
Residual	20.377	38	0.536					
'Downstream' Site Group *Log (n+1) D. r. bugensis density*:								
Regression Model (all Sites)	7.793	2	3.896	7.702	0.003**			0.275
+ Stream depth (cm^{-1})					0.003**	0.034	0.447	
+ % Gravel in total substrate composition					0.024*	0.057	0.332	
Residual	20.545	37	0.555					

Discussion

Across the study reach, variation of *D. r. bugensis* density was most strongly associated and negatively correlated with distance from the species' upstream limit. Despite clear variation of environmental conditions between study sites; the only other factor associated with *D. r. bugensis* density across the reach was stream depth, which was positively correlated. According to regression, stream depth predicted *D. r. bugensis* densities at weaker significance and explained a smaller proportion of variation (p = 0.048; r^2 = 0.05) compared to distance from the species' upstream limit (p = <0.001; r^2 = 0.28). This suggested a dominant factor for

D. r. bugensis distribution across the study reach was distance from the species' upstream limit; considered to be an outlet shaft servicing Wraysbury Reservoir (**Chapter 2**; 30 pp.). In this respect, findings complimented those of Stanachkova et al. (2015) who recently observed increased likelihood of lotic *D. r. bugensis* establishment with proximity to reservoir systems in Bulgaria. Notably, a series of other lotic invasive species have been associated with source populations from artificial reservoirs: including Prussian carp *Crassius gibelio* in Turkey (Tarkan et al. 2012), Australian crayfish *Cherax quadricarinatus* in Singapore (Ahyong and Yeo 2007) and Ponto-Caspian Amphipod *Dikerogammarus villosus* in the UK (MacNeil et al. 2010).

It was considered whether decline of *D. r. bugensis* density with downstream distance was related to ongoing dispersal of *D. r. bugensis* veligers by the outlet shaft from Wraysbury reservoir. While to our knowledge, no recent benthic surveys of the reservoir had been undertaken; large *Dreissena* spp. densities (>10,000 individuals m^{-2}) have been found in other UK and European reservoirs (Orlova et al. 2005; McLaughlan and Aldridge 2013; Stanachkova et al. 2015). If suspended *D. r. bugensis* veligers, sourced from reservoir populations could enter Wraysbury River via the outlet; greater populations might be expected to develop nearer this facility. Further, if *D. r. bugensis* veliger mortality was relatively high in the lotic environment of Wraysbury River (e.g. due to stream solar exposure (Seaver et al. 2009; Thaw et al., 2014), lack of suitable benthic substrate for settlement (Mellina and Rasmussen 1994; Karatayev et al. 1998), inhibitory flow velocities (Hovarth and Lamberti 1999; Ackerman 1999), then greater recruitment would feasibly occur closer to the stream entry point from the reservoir, where stream veliger concentrations would be highest.

However, information on the shaft facility at Wraysbury River (Pers. Comms Thames Water 2018) suggests this feature has only remained an emergency valve for catastrophic failure (accordance to UK Reservoirs Act 1975); with reservoir water only released for short durations

once every five years in statutory, operational tests (outflow for < 30mins; see: DEFRA 2006). While it is likely the first establishment of *D. r. bugensis* in Wraysbury River was due to such a procedure; the infrequency and short duration of operational testing suggests *D. r. bugensis* populations in the river would not be significantly facilitated by veliger inputs from the Reservoir. With mean *Dreissena* spp. life span assumed to be 3.5 years (Morton 1969; O'Neill and MacNeill 1991) and shorter than the time between valve tests; it was considered likely mussel populations in Wraysbury River have been self-sustaining rather than dependent on the outlet shaft.

Higher mussel densities at upstream sites may thus be driven simply longer legacy of *D. r. bugensis* establishment compared to sites downstream. In explanation, *Dreissena* spp. veliger propagules have been shown to radiate with downstream flows (Griffiths et al. 1991; Bobeldyk et al. 2005); suggesting *D. r. bugensis* nearer their upstream limit were present longer in Wraysbury River, with more time to develop higher density populations. It also follows that the greatest source of *D. r. bugensis* veliger propagules produced in Wraysbury River would be from the largest adult populations in the upstream reaches. If veliger mortality increased with downstream distance travelled (See: Hovarth and Lamberti 1999; Rehmann et al. 2003); higher propagule survival rate and growth of new adults would occur nearer the source, upstream population. With provision of similar environmental conditions downstream; *D. r. bugensis* may still reach comparable densities under a downstream march model (*sensu* Hovarth et al. 1996); however further monitoring would be required to assess the rate of spread.

Within site groups, *D. r. bugensis* were associated with a wider range of stream physical parameters than when tested across the whole reach. For example, *D. r. bugensis* densities were best explained by stream depth in the upstream site group (sites 1-2) with significant, positive correlation (p = <0.001). This mirrored findings from deep lentic systems of North America where increased depth has been associated with reduced *Dreissena* spp. predation by waterfoul

(Petrie 1999) and greater protection of larval veligers from damaging Ultra-Violet Radiation (Seaver et al. 2009; Thaw et al., 2014). However, Wraysbury River was unlikely to be comparable with such environments and we did not find evidence of mussel predation or relationships of density with stream solar exposure in our study. Instead, increased stream depth could be associated with reduced stream velocity compared to elsewhere in the channel. For example, reduced velocities, particularly at near bed level, might not supersede those shown inhibitory to mussel feeding (i.e. >0.2m $^{-2}$; Ackerman 1999) and could promote increased settlement of suspended larval veligers through reduction of flow turbulence in deeper sections (Hovarth and Lamberti 1999; Rehmann et al. 2003). While we did not detect relationships of mussel density with stream flows, our measures were at 0.6 depth. Stream velocity at bed level could more effectively demonstrate such effects in future study.

A second parameter shown to predict *D. r. bugensis* density within the upstream site group was the percent contribution of cobbles to substrate composition. While weaker than for stream depth, this parameter was again, positively correlated to mussel density with strong significance ($p = 0.009$). Compared to smaller clast size classes, cobbles are widely considered to be provide optimal surface for mussel byssus attachment (Mellina and Rasmussen 1994; Berkman et al. 1998; Karatayev et al. 1998; Nalepa et al. 2003) and in lotic systems, more hydraulically stable substrate for epifaunal benthos (Quinn and Hickey 1990; Cobb et al. 1992). While it was surprising similar trends were not found within the midstream and downstream site groups; other factors may have confounded *D. r. bugensis* establishment at these sites. For example, the site with the highest proportion of substrate as cobble clast sizes (Site 9: 43%) was located far from the upstream limit of *D. r. bugensis* (distance). Under previously discussed downstream march mechanics, it was possible that insufficient time had passed since first invasion for representative *D. r. bugensis* densities to establish at these sites. Dominance of

cobble substrate at site 9 for example, could mean larger populations develop there in future if substrate conditions remain analogous.

Within the midstream site group, *D. r. bugensis* density appeared to be predicted by stream longitudinal velocity with moderately significant, positive correlation (p = 0.004). This was surprising because *Dreissena* spp. have been suggested to favour low flow environments where damage to suspended larval veligers may be reduced (Hovarth et al. 1999; Lucy et al. 2008) and suspension feeding is not inhibited due to flow pressures (Ackerman 1999). With a mean range of 0.17 – 0.22 m s^{-1} measured at 0.6 depth across midstream study sites; flows may not have been sufficient to cause such limitations for the species. Provided bed-level flows in Wraysbury River were below inhibitory rates; relatively increased velocities may have instead promoted greater water oxygenation (Philipson 1954; Quinn and Hickey 1990) and cycling of suspended food materials (Riisgaard et al. 2004; Dame 2012) alongside the prevention of siltation, shown to be problematic for *Dreissena* spp. establishment elsewhere (Karatayev et al. 1998). More detailed observations of near bed flows, suspended seston transport and siltation dynamics would be required to better evaluate the influence of stream velocity on *D. r. bugensis* at these sites.

For the downstream site group, *D. r. bugensis* density was predicted by stream depth with which it was positively correlated with moderate significance (p = 0.003). Given similar associations for this parameter both within the upstream site group and across the whole reach; stream depth appeared an important secondary factor in *D. r. bugensis* distribution in Wraysbury River (aside distance from the species' upper limit). That deeper stream sections may facilitate *D. r. bugensis* has previously been discussed and could explain such variance in the downstream study sites. However, we also found a positive, significant correlation of *D. r. bugensis* with the proportion of gravel in substrate composition at this site group (p = 0.024). This was unexpected because *Dreissena* spp. have been typically associated with larger clast

sizes (Mellina and Rasmussen 1994; Strayer 1996; Katatayev et al. 1998), such as that of cobble for our upstream site group. For epifaunal taxa, gravel is a less stable bed material with greater risk of hydraulic scour than larger clast sizes (Quinn and Hickey 1990; Cobb et al. 1992). It was expected this substrate type would be suboptimal for *D. r. bugensis* due to risk of displacement. However, during previous work in this project we have shown *D. r. bugensis* in Wraysbury River may form byssus attachments to multiple gravel clasts, developing a root like substrate-byssus agglomerate to anchor in the bed (See: **Figure 3.1**; **Chapter 3**; 57 pp.). It is possible that through this trait *D. r. bugensis* may stabilise gravel beds as an ecosystem engineer (*sensu* Gutiérrez et al. 2003); allowing the species to readily establish under wider physical bed conditions than previously assumed.

The positive association of *D. r. bugensis* density with different, apparently contradictory physical parameters across upstream, midstream and downstream site groups suggests a variety of stream physical conditions may provide suitable environment for *D. r. bugensis* establishment. For example, increased stream depth at our upstream and downstream sites may attenuate flows for optimal feeding rates and promote larval veliger settlement. On the other hand, higher velocity stream conditions in our midstream sites could provide oxygenation, food cycling and protection against siltation for *D. r. bugensis*. Considering too, the highlighted trait of gravel agglomeration with mussel byssus; results show *D. r. bugensis* as a versatile invader in the shallow, lotic environment of Wraysbury River. Several factors expected to negatively correlate with mussel density, such as increased stream solar exposure and flow velocities, were also not found to do so in our study.

While in other rivers, a series of factors unacknowledged in this study may also impact *D. r. bugensis* success such as stream food availability and quality (Fanslow et al. 1995; Schneider et al. 1998), calcium carbonate concentrations (Hincks and Mackie 1997; Whittier et al. 2008) and predation by waterfowl or crayfish (Martin and Corkum 1994; Petrie and Knapton 1999;

Reynolds and Donohoe 2001); this work provides an important benchmark for future study on *D. r. bugensis* distribution as the invasion progresses.

Provided establishment of *D. r. bugensis* at an upstream source such as from the reservoir shaft in our study; it is feasible invasions could occur in similar regional habitats. Other Thames tributaries with proximal reservoirs may be at particular risk. Examples include reaches of Colne Brook (near the Wraysbury Reservoir; Long: 51.460804, Lat: -0.538104), the River Mole (near the Island Barn Reservoir; Long: 51.390827, Lat: -0.364739), River Ash (near the Queen Mary Reservoir; Long: 51.406077, Lat: -0.457870) and River Lea (near the King George Reservoir; Lat: 51.644205, Long: -0.012522). To alleviate biosecurity risk at such sites, aquatic resource managers may make efforts to monitor locally for *D. r. bugensis* while imposing stronger biosecurity measures for statutory water releases with reservoir shaft testing. Alongside the apparent release of *D. r. bugensis* to Wraysbury River; similar tests have been associated with the spread of killer shrimp *Dikerogammarus villosus* into an outlet of Grapham Reservoir, Cambridgeshire (Environment Agency, Pers. Coms. 2011). Results of this study suggest greater care should be taken to manage invasive species risks in such cases. Considering too, planned water authority introductions of increasing water transfer pipes between river catchments for operational resilience (Hutchins and Bowes 2018); accompanying biosecurity measures should be prioritised for restricting further spread of invasives such as *D. r. bugensis*.

Conclusions

1. Across the study reach, increasing densities of *D. r. bugensis* appeared most strongly associated and negatively correlated with distance from the species' upstream limit; being a local reservoir water release valve. Though thought to be the source of mussel populations in

Wraysbury River, the reservoir valve was not thought to explain higher proximate mussel densities as a potential source of veligers. Instead, relative longevity of *D. r. bugensis* presence at upstream sites could have permitted development of greater upstream populations than downstream; perhaps benefitting from increased suitable substrate availability from *Dreissena* shells already present. More generally, mussel densities appeared to increase throughout the study reach compared to 2015-16 study and downstream trends in density, compared to 2015-16, suggested a degree of downstream march for the species since this time.

2. *D. r. bugensis* density was also positively associated with stream depth across the study reach, though this was less important for explaining trends compared to proximity to the species' upstream limit. Considering previous literature, greater stream depth may have provided optimal flow conditions for *D. r. bugensis* veliger survival and subsequent settlement, alongside reduced inhibition of adult mussel feeding. Further research would be needed to clarify these dynamics.

3. Within the upstream site group alone, *D. r. bugensis* was shown to be positively associated with stream depth and the percent cobble contribution to substrate composition. Both parameters complimented previous literature on the species; unlike at the midstream site where higher stream velocities were shown in positive correlation. Within the downstream site group stream depth was again positively associated with *D. r. bugensis* density alongside the percent gravel contribution to substrate composition. The latter factor was again surprising given positive literature associations of *Dreissena* spp. with larger clast sizes; however the documented ability of *D. r. bugensis* to use byssus to bind several gravel clasts as an anchor on the bed (**Chapter 4**; 82 pp.) demonstrated versatility of the species across different substrate typologies.

4. In general, *D. r. bugensis* densities appeared to be well established and with increasing populations throughout Wraysbury River compared to previous study. Clearly the species was able to establish across a wider range of physical conditions than might be expected from previous literature. While the highest potential densities for the species in this river remained uncertain, future study could elucidate this, monitoring the point at which populations peak at sites in the study reach.

5. Provided successful initial establishment, we conclude that the species may successfully become invasive in similar regional environments. Thames tributaries with reaches in proximity to reservoirs could be at particular risk given the apparent introductory role of the reservoir outlet shaft at this site. Greater monitoring and biosecurity efforts during future water transfers could reduce risk of further spread at such sites.

Chapter 8. *Study Synthesis and Final Conclusions*

Prior to establishment, *D. r. bugensis* was considered the most threatening invasive species to UK biodiversity (Roy et al. 2014). Concerns were primarily driven by invasion histories in other environments. For example, *Dreissena* spp. had been shown to significantly impact physical bed characteristics (Stewart et al. 1998; Ward and Ricciardi 2007), alter concentrations of suspended seston (Stewart and Haynes 1994; Horgan and Mills 1997) and support commensal relationships with other Ponto-Caspian invasives (Ricciardi 2001; Gallardo and Aldridge 2015). In particular, significant restructuring of benthic invertebrate communities had been associated with such factors following late 20th century *Dreissena* spp. invasions of the North American Great Lakes region (Stewart and Haynes 1994; Ricciardi et al. 2001; Beekey et al. 2004) and a series of European canal and lake networks (Burlakova et al. 2005; Yakovleva and Yakovlev 2011).

Increased invertebrate density and taxonomic richness had been observed in other invaded environments following *Dreissnea* spp. invasions (Ricciardi 2003; Ward and Ricciardi 2007; Burlakova et al. 2012). Specifically, groups of Amphipoda spp. and Gastropoda spp. were shown to benefit due to increased substrate surface area (MacIsaac 1996; Ricciardi et al. 1997; Bially and MacIsaac 2000) alongside predator (González and Downing 1999; Ward and Ricciardi 2007) and flow refugia (Ricciardi et al. 1997) provided by mussel beds. Likewise, major groups like dipteran Chironomidae spp. were thought to utilize mussel pseudofacaes deposits as food resources (Griffiths 1993; Botts et al. 1996). Impacts of invading *D. r. bugensis* on benthic invertebrates were generally thought to be facilitative; though some taxonomic groups of conservation importance had been threatened with decline (Stewart et al. 1998; Ricciardi et al. 2007). Notably, significant losses of native Unionidae spp., had been found due to Dreissenid smothering and competition for space resources (Ricciardi et al. 1998; Sousa et

al. 2011). In addition, reduction of water column phytoplankton communities were strongly associated with mussel feeding (Stewart and Haynes 1994; Horgan and Mills 1997).

Despite such histories, initial investigation of *D. r. bugensis* in the known UK range, a 2km^{-1} reach of Wraysbury River, Surrey (Lat 51.45225; Long -0.520528), failed to identify any expected impacts on cohabiting ecology. A May 2015 – May 2016 survey suggested *D. r. bugensis* constituted ~43% of total mean benthic biomass at this site; however, a limited response was found from cohabiting benthic ecology. For example, invertebrate density and taxonomic richness appeared similar across a series of homogenous lotic sites, despite significant variation in cohabiting *D. r. bugensis* density. Further, where reduction in invertebrate density and taxonomic richness was found, the highest *D. r. bugensis* densities were recorded. The latter results contrasted to those in the literature (see: Ward and Ricciardi 2007); implying generally deleterious rather than facilitative associations of *D. r. bugensis* with cohabiting ecology. If supported by subsequent studies in this thesis, findings could have evidenced unusual impacts of *D. r. bugensis* in the invaded UK range.

However, more controlled stream experiments in summer 2017 gave contradictory results to that first survey and were more synonymous with literature expectations. A series of novel artificial substrates were deployed, designed to simulate higher *D. r. bugensis* densities than currently found in Wraysbury River (at this point, still containing the known UK range). Left for periods where invertebrate communities could naturally colonise, the comparative response of benthic taxa to increasing mussel shell treatments across artificial substrates was measured. Observations implied clear facilitation of communities on substrates with higher densities of *D. r. bugensis* shells. Notably, consistent, statistically significant increases to invertebrate density and richness were found only on the highest substrate shell treatments. These simulated mussel densities of approximately 2200 *D. r. bugensis* individuals m^{-2}; much higher than the maximum mean value found for any invaded sites during the initial 2015-16 monitoring study

(130 individuals m^{-2}). It was suggested natural *D. r. bugensis* densities would need to increase by an order of between 8-15 times to cause comparable natural impacts on benthic ecology in the known UK range.

Similarly, the influence of *D. r. bugensis* on stream geomorphic processes were shown to be dependent on mussel density. When a test-bed was exposed to high flow conditions, *D. r. bugensis* densities equivilant to 250 individuals m^{-2} significantly reduced bedload transport rates compared to those of 125 and 0 individuals m^{-2}. In a second flume experiment, based on flow conditions similar to those measured in Wraysbury River; again, only mussel densities of 250 individuals m^{-2} were consistently associated with changes to near bed flow velocities and stream turbulence.

To the author's knowledge, geomorphic impacts of *Dreissena* spp. had not been investigated elsewhere; though it was suggested cohabiting ecology might be affected by mechanisms in evidence. For example, conditions of reduced bedload transport and flow refugia could benefit invertebrate taxa by reducing rates of involutary drift, facilitating oviposition and scraper feeding practices. For fish, more stable bed materials could result in reduced bedload abrasion for juveniles and provide favourable conditions for certain benthiverous taxa. Finally, higher stream flow turbulence caused by increased substrate roughness due to mussel beds might help recirculate bed sediments, increasing oxygenation and nutrient distribution to surrounding benthos.

Additional research would be required to elucidate whether *Dreissena* spp. could cause geomorphic impacts in natural UK envirionments. However, our experiments suggested mean densities of at least 250 *D. r. bugensis* individuals m^{-2} could be required to consistently observe such mechanisms in the current invasive range. Again, this value was higher than found for natural *D. r. bugensis* populations recorded in Wraysbury River between 2015-2016

(maximum: 130 individuals m^{-2}; mean: 54 individuals m^{-2}); suggesting *D. r. bugensis* populations would need to expand before impacts on cohabiting ecology were observed.

Mussel density also appeared an important determinant for impacts of *D. r. bugensis* suspension feeding. Initially, it was thought *D. r. bugensis* in Wraysbury River could cause reduction of suspended seston concentrations through this mechanism. Such impacts had been widely recorded in North American Great Lakes region (Fanslow et al. 1995; Strayer et al. 1999); resulting in significant changes to cohabiting benthic (Stewart and Haynes 1994; Kuhns and Berg 1999) and phytic (Pothoven et al. 2001; Maguire and Grey 2006) communities across various tophic levels (Stewart and Haynes 1994; Ward and Ricciardi 2007). However, we failed to present clear downstream changes to organic or mineralogic stream seston concentrations when monitoring lotic reaches of Wraysbury River between 2015-16.

Considering the literature, further field observations at Wraysbury River and a series of *in situ* and *ex situ* pilot experiments (Summer 2018); it was thought factors of stream flow and water column mixing could limit impacts of *D. r. bugensis* suspension feeding in rivers (*Sensu* Strayer et al. 1999; Dame et al. 2012). It was crudely estimated mussel populations would have to reach continuous mean densities of 376 individuals m^{-2} over a 2km reach of the Wraysbury River in order to filter 100% of the water column through suspension feeding. Even then, effects would be reliant on zero allochthonous or autochthonous inputs and a hydraulic state of total stream mixing. Given 2015-16 measures of mean mussel density showing only 54 individuals m^{-2} throughout the Wraysbury River; it was again thought likely that increased mussel populations would be required before any such impacts were observed at the reach scale.

Together, aforementioned investigations suggested a holistic variety of post-invasion ecological impacts from *D. r. bugensis* could be expected between 2 to 15 times the maximum

population densities known in the UK. It remained uncertain whether such densities were possible, -at least within the known invaded range (at the time, the 2 km^{-1} reach of Wraysbury River). At a glance, these results implied impacts from *D. r. bugensis* might not be as potent nor threatening to native biodiversity than had been suggested (e.g. Roy et al. 2014). However, two final investigative chapters of this dissertation suggested caution should be taken with this view.

In summer 2017 the discovery of Ponto-Caspian *Dikerogammarus* spp. shrimps in Wraysbury River drove concern that *D. r. bugensis* may facilitate establishment of other Ponto-Caspian invasives. For *Dreissena* spp., mechanisms implied to cause this under 'Invasional Meltdown Hypothesis' (*sensu* Simberloff and Von Holle 1999) had been suggested with several studies citing commensal relationships between *Dreissena* spp. and a series of other Ponto-Caspian taxa (Ricciardi 2001; Kobak 2014; Gallardo and Aldridge 2015). To this author's knowledge, little research had explicitly tested for such associations *in situ* (but see: Ricciardi 2001), -much less for regions of the UK.

An investigation into the distribution of invasive and native invertebrates at a site in the Norfolk Broads was prompted at one of a few known sites where Ponto-Caspian *Dikerogammarus* spp. and *Dreissena* spp. had cohabited for over 5 years (see: NNSS 2012). Results provided evidence for Invasional Meltdown processes by *Dreissena* spp. in a UK freshwater environment. Native invertebrate groups expected to benefit from *Dreissena* spp. did not show positive relationships with increasing mussel density. However, significant, positive associations of *Dikerogammarus* spp. and another Ponto-Caspian amphipod, *Cheliocoropohium curvispinum* density were widely recorded.

The Norfolk Broads study site (Long: 52.739205, Lat: 1.497049) was limited in geographic comparability to that of Wraysbury River; however, findings represented the first quantitative,

field-based evidence that invasive *Dreissena* spp. more strongly facilitated populations of Ponto-Caspian invasives when compared to native taxa. The precise mechanisms of such impacts could not be elucidated; however, mean *Dreissena* spp. densities across invaded sites in the Norfolk Broads were 554 individuals m^{-2}, only 4-5 times greater than the highest found fo *D. r. bugensis* in Wraybsruy River during 2015-16 (130 individuals m^{-2}). If Invasional Meltdown processes were primarily dependent on *Dreissena* spp. densities (as apparent for other impacts in this study); the risk of such effects could increase with further proliferation of *D. r. bugensis* in the UK.

Notably, the final data chapter of this dissertation suggested future increases of *D. r. bugensis* population density might occur both within the current invaded range and elsewhere. Work undertaken in summer 2018 assessed *D. r. bugensis* ecological habitat preferences in the Wraysbury River. It was found that within upstream, midstream and downstream sites, the species was able to establish across a wider range of physical conditions than might be expected from previous literature. This suggested establishment of *D. r. bugensis* in similar UK environments, particularly those associated with reservoir outlets, may readily occur in future. In addition, observations showed *D. r. bugensis* density across the known invaded range had increased substantially since similar measurements in 2015-16. For example, mean densities across the same $2km^{-1}$ reach of the River Wraysbury had increased from 54 to 122 individuals m^{-2}, with the maximum mean value at any site increased from 130 to 314 individuals m^{-2}. If mussel populations continued to rise in future; impacts of *D. r. bugensis* discussed elsewhere in this thesis would clearly become more likely.

During the last year of this PhD study, the known range of *D. r. bugensis* also clearly expanded. The mussel was found at Richmond during volunteer surveys of the River Thames (November 2017), approximately 30 km^{-1} downstream of Wraysbury River (See: **Introduction**; **Figure 1.2**; 25 pp.). Maximum mussel densities at this site were only 20 individuals m^{-2} (ZSL pers.

comms), though populations could increase with time. For example, the large, deep and turbid River Thames was more characteristic of systems shown to be heavily invaded by *Dreissena* spp. in the North American Great Lakes literature (see: Howell et al. 1996; Strayer et al. 1996; Nalepa et al. 2009). This environment could provide favourable conditions for *D. r. bugensis* compared to Wraysbury River; including greater availability of hard substrate, reduced near-bed flow velocities and increased suspended seston availability for food resources. In addition, concrete embankments, associated with *Dreissena* spp. colonisation in European canals (Aldridge 2014), remain common features on the River Thames; while frequent recreational and industrial boating traffic (see: Jackson and Grey 2013) could facilitate further spread of *D. r. bugensis* elsewhere in the catchment.

Favourable environmental conditions and human activities like recreational boating may have contributed to the establishment of another invasive bivalve in the Thames catchment: the Asiatic clam *Corbicula fluminea*, first recorded in 2004 (Elliott and Ermgassen 2008). This species was later shown to have a large invaded range across southern, central and eastern English rivers, interconnected by canal boat networks (Elliott and Ermgassen 2008). To the author's knowledge, no studies have examined *C. fluminea* impacts on ecology in such environments. However, aforementioned River Thames volunteer surveys (November 2017) in Richmond (Grid Lat 51.449178; Long -0.305301) found maximum *C. fluminea* densities of 756 individuals m^{-2}; contributing to 65 % of total invertebrate abundance recorded at the site (ZSL pers. comms. 2017). If *D. r. bugensis* were to reach similar population densities over time, impacts on cohabiting benthic ecology through various mechanisms discussed in this dissertation would again, be more likely.

Unfortunately, temporal limitations of this thesis were significant because work could only elucidate early-stage invasion dynamics. Being undertaken so soon after the first UK record of *D. r. bugensis* (see: Aldridge 2014); a limited number of natural *D. r. bugensis* populations

could be studied, by necessity. For example, at the point of finalising this dissertation, the only known population of *D. r. bugensis* greater than 20 individuals m^{-2} was still located in the $2km^{-1}$ reach of Wraysbury River. In future, lentic environments in particular, may present favourable conditions for high density invasive populations, as suggested in North American studies (Howell et al. 1996; Nalepa et al. 2009). Range expansion and ecological impacts of *D. r. bugensis* may thus be more likely to occur in UK lakes rather than rivers. It remains unfortunate that while current establishment of *D. r. bugensis* in Wraysbury Reservoir, local to the Wraysbury River (Long 51.461206, Lat -0.525728) has been suspected (Aldridge 2014); populations at this site remain formally unconfirmed. If *D. r. bugensis* were present, future investigations could allow comparison of invasion dynamics across lotic and lentic UK systems.

Immediate gaps in knowledge also pertain to the distribution and potential impacts of *D. r. bugensis* across the wider River Thames catchment. Firstly, regular boat-based monitoring with equipment such as ponar grab samplers and dredging nets could clarify range expansion of *D. r. bugensis* since the outset of this study. Building on approaches used in this thesis, *in situ* artificial substrates could help elucidate potential ecological impacts where *D. r. bugenis* were found. Similarly, further flume experiments could help clarify the influence of *D. r. bugensis* on geomorphic mechanisms in such environments. For example, a greater variety of substrate grain mixtures, more representative of naturally occurring river sediments, could be tested. Likewise, the role of mussel suspension feeding in natural environments could be further investigated. Aside *in situ* monitoring of seston concentrations at sites of *D. r. bugensis* establishment; additional flume-based studies could be conducted on *D. r. bugensis* feeding rates across different seston mixtures natural to various Thames environments. Finally, co-distribution and commensal associations of *D. r. bugensis* with other Ponto-Caspian invasives could be monitored throughout the catchment to elucidate voracity of the 'Invasional

Meltdown' issue. Broadly speaking, each aspect of study within this dissertation could be further built-on across time and space to better assess invasion dynamics and ecological impacts of *D. r. bugensis* in the UK.

It is hoped such work contributes to scientific understanding of invasive *D. r. bugensis* populations in the UK, particularly for small lotic environments. Four years after the first record of D. r. bugensis, there have been no clear impacts on cohabiting ecology and the most significant known population of the species still occurs within the original invaded range. As such, it currently appears difficult to support the species' assignation as the most potentially threatening invasive species to UK biodiversity (Roy et al. 2014). However, given observations of increasing mussel densities and recent expansion into the wider River Thames catchment; the influence of *D. r. bugensis* on cohabiting ecology may increase with time. Specifically, potential impacts due to mussel shell-bed structures, suspension feeding, geomorphic influences and interactions with other Ponto-Caspian taxa have been evidenced herein. Given such a wide range of structuring mechanisms for freshwater communities, scientific investigations on *D. r. bugensis* in UK freshwaters should continue with vigilance.

While the focus of this thesis was to investigate impacts of *D. r. bugensis* on cohabiting ecology in UK rivers, it is also hoped the findings contribute to invasion management of the species. For example, in threatened environments where *D. r. bugensis* is yet to be recorded, this work may indirectly stimulate improved detection rates and justify better biosecurity protocols to prevent downstream spread. Further, where *D. r. bugensis* is known to be present, evidence concerning its potential impacts on ecology may galvanise and inform timely intervention to reduce population densities. Discussed further in the following, these contributions may help limit both the spread of invasive *D. r. bugensis* and associated impacts. Ideally, progress in these areas will result in improved conservation outcomes for native UK freshwater ecology threatened by *D. r. bugensis*.

Firstly, invasive *Dreissena* spp. have been widely considered to favour lake, reservoir and deep river/canal environments. This for example, has been noted in advisory documents published by the UK Government's invasive species authority (Non Native Species Secretariat 2015) and supported by various field studies outside the UK (e.g. Strayer 1991; Johnson and Padilla 1996; Matthews et al. 2013; Karatayev et al. 2015). By highlighting and describing expansive populations in a shallow, gravel-bed river (e.g. Chapters 2 and 7; 96 pp., 189pp., respectively); this thesis has underlined broader habitat flexibility of *D. r. bugensis* than expected (explored in Chapter 7; 179-202 pp.). It follows that field-practitioners who read this work, for example in associated publications (Mills et al. 2017; 2019), may more readily interrogate suspect specimens, regardless of their environmental context. Also, that future monitoring efforts, including those made by this author, may be encouraged to screen for invasive *D. r. bugensis* populations over a wider geographical and environmental range. This may contribute to improved detection rates of newly established *D. r. bugensis* populations, providing more rapid understanding of the species' current UK range.

The UK Government's Invasive Non-native Species Strategy (DEFRA 2015) emphasises the importance of rapid determination of an invasive species current range to facilitate timely management for preventing population expansion. This may be of particular relevance for riverine aquatic species, because lotic systems act as highly efficient pathways for invasive propagules (Leuven et al. 2009; Leprieur et al. 2008; Francis and Chadwick 2013). For example, as found for other high-profile fauna in the UK like the American signal crayfish *Pacifastacus leniusculus* (Rosewarne et al. 2013; Holdich et al. 2014), killer shrimp *Dikerogammarus villosus* (Bij de Vaate et al. 2002; Gallardo et al. 2012), and topmouth gudgeon *Pseudorasbora parva* (Pinder et al. 2005; Britton et al. 2010). Only given sound understanding of these species' local distribution, have management interventions isolated or reduced an invasive population, thus reducing chances of downstream expansion. Management

interventions considered for these species have included deliberate retention/construction of weir impoundments alongside manual removal programmes (Gherardi et al. 2011; Rosewarne et al. 2013; American Signal Crayfish), geographically targeted public advertisement campaigns to 'check, clean and dry' recreational equipment (Madgwick and Aldridge 2011; Anderson et al. 2014; Killer Shrimp) and biocidal removal of major upstream, propagule sources (Britton and Brazier 2006; Britton et al. 2008; Topmouth Gudgeon). Given sound geographic understanding of the UK *D. r. bugensis* range, similar interventions may be attempted to isolate and reduce these populations. Notably, observations from this thesis demonstrate at least one potential trail location for *D. r. bugensis* in the UK.

For example, field studies herein highlight a relatively short ($1.8km^{-1}$) reach of the Wraysbury River ($<2.0km^{-1}$; Lat 51.45225; Long -0.520528) containing the highest known density of *D. r. bugensis* in the UK (See most recent observations, Chapter 7, summer 2018; 189 pp.). This population may be an important propagule source for *D. r. bugensis* expansion into downstream environments; containing sites with mussel densities orders of magnitude higher than any other location studied. Now identified, this reach could be selected for targeted management by UK environmental authorities. In this respect, recent trials of manual removal, shock-treatment and biocide application methods have been made for invasive macrophytes (e.g. Alexander et al. 2008; Caffey 2010; Coughlan et al. 2018*a*; Crane et al. 2018) and benthic fauna, including Asiatic clam (e.g. Gomes et al. 2014; Sheehan et al. 2014; Coughlan et al. 2018*b*) American signal crayfish (Peay 2014; Green et al. 2018; Peay et al. 2019) and zebra mussel (Durán et al. 2010; Costa et al. 2011; Meehan et al. 2013); adding to options already discussed (above). Building on this progress, similar trials for managing *D. r. bugensis* populations might feasibly be undertaken in densely populated reaches of Wraysbury River identified in this work, including by this author and partnered scientists.

With regards to management for reducing downstream invasion risk further, it is hoped observations from this thesis will also caution need for improved biosecurity management at reservoir facilities. It was shown for example, the range of *D. r. bugensis* in Wraysbury River was limited to lotic environments downstream an outlet valve servicing a nearby reservoir (release-tested once every 5 years under the UK Reservoirs Act (1975)). As discussed (Chapters 2, 7; 34, 184 pp., respectively), establishment of *D. r. bugensis* in Wraysbury River was thought to result from discharge of veliger-contaminated reservoir water from this feature. Given that unlike the reservoir, Wraysbury River is connected to other watercourses (joining the Rivers Thames c.2.8km downstream from the reservoir outlet valve); it can be surmised the reservoir release valve at this site provided a pathway for the mussel to enter the wider Thames catchment, placing downstream environments at heightened risk of *D. r. bugensis* invasion. Further discussed in Chapter 7 (200 pp.), a similar mechanism of range expansion was evidenced for invasive killer shrimp *Dikerogammarus villosus* found downstream of an emergency release valve servicing Grapham Water reservoir, Cambridgeshire, UK (Environment Agency, Pers. Coms. 2011). Such episodes, now evidenced at multiple sites (with the addition of this work), should act as important 'cautionary tales.' Namely, to justify improved biosecurity standards at such facilities.

For example, interventions could be made to ensure reservoir release valve tests under the UK Reservoirs Act 1975 take place under conditions of greater control, where water is captured rather discharged into downstream environments. Such management action appears instinctively practicable and may prevent downstream spread of *D. r. bugensis* and/or other invasive species from similar sites elsewhere. Notably, comparable 'end of pipe' biosecurity considerations may become increasingly relevant following recent UK Government recommendations to increase use of cross-catchment transfers for drinking water supply resilience in the UK (DEFRA 2018; OFWAT 2019). This thesis presents additional evidence

to underline risks of invasive species propagation from such artificial, industry-driven catchment connections; suggesting significant caution may be needed with these water management approaches in future.

Concerning environments already invaded by *D. r. bugensis*, this thesis as discussed (204-208 pp.), includes a series of baseline studies demonstrating potential *D. r. bugensis* impacts on cohabiting ecology. In summary, it was shown that *D. r. bugensis* shells can significantly restructure benthos communities (see: Chapter 3; 57-80 pp.) including through potential facilitation of other invasive species (see: Chapter 6; 152-178 pp.). Further, that under certain conditions, *D. r. bugensis* populations may alter habitats by impacting stream substrate stability, near-bed flow conditions (see: Chapter 4; 82-111 pp.) and seston concentrations (see: Chapter 5; 112-152 pp.). These findings affirm concerns that in UK freshwaters, *D. r. bugensis* may significantly impact cohabiting ecology through various mechanisms (see: Roy et al. 2014); of which none had been previously tested in UK-based field or laboratory experiments. To add, some mechanisms, such as mussel biogeomorphic impacts, had not been previously discussed in the extensive *Dreissena* spp. literature; despite similar, invasive 'ecosystem engineering' traits already treated with concern for other species (e.g. crayfish burrowing; Herborg et al. 2003; Crawford et al. 2006; Harvey et al. 2014).

Given such a range of evidenced impacts, it is again hoped that broadly, these findings provide impetus for concerted management action to minimise *D. r. bugensis* populations in UK freshwaters. However, considering financial pressures that limit biodiversity conservation efforts (McCarthy et al. 2012; Waldron et al. 2013); this data may also contribute to bespoke, cost-efficient interventions where the mussel is already present. For example, in artificial substrate experiments (Chapter 3; 57-81 pp.) significant impacts to benthic community were primarily found at *D. r. bugensis* shell densities of $2200m^{-2}$. In a situation with limited funding availability for environmental managers, sites with mussel densities at or above this value could

be prioritised above others for treatment. Targeted efforts to reduce high density *D. r. bugensis* populations (e.g. using aforementioned approaches; 213 pp.) could therefore limit their impacts where likely most acute; achieving conservation outcomes for greater cost-efficacy.

However, and in line with caveats mentioned throughout this project, it should be noted the *D. r. bugensis* densities sufficient for significant ecological impacts (across various mechanisms studied) remain somewhat uncertain. For management and conservation guidance, the findings of this project would currently be of limited use, particularly across widely different environmental conditions to those tested (e.g. upland, large and low-alkalinity rivers; lakes, ponds, reservoirs). However, as a starting point, this thesis provides at least approximate relationships of mussel density with impact magnitude concerning some mechanisms, particularly for small rivers. Future research, including that already planned by this author, should work to refine understanding of *D. r. bugensis* impacts across other environments. In the longer term, additional data could support models to predict structural change for cohabiting ecology across different environments (e.g. Gallardo and Aldridge 2013b; Gallardo and Aldridge 2015). Progress in such areas would permit increasingly informed management decisions, including further cost-effective intervention at sites where *D. r. bugensis* were considered likely to cause undesirable impacts for cohabiting ecology.

In summary, the work of this thesis may be considered an opening step towards more informed management of invasive *D. r. bugensis* in UK freshwaters. Other scientists, if they so wish, may freely repeat any aspect of this work, perhaps further adapting the novel experimental approaches described for the artificial substrate and flume-based studies. By whatever route, it is the sincere wish of the author that this thesis encourages more research on invasive *D. r. bugensis* impacts and ultimately, contributes to the conservation of threatened freshwater environments.

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APPENDIX 1. Taxa list with mean annual abundance (individuals m^{-2}) per site and total mean annual biomass (dry mass as g m^{-2}) across all sites. The source of biomass length-weight equations are also noted. All mean annual abundance values have been rounded to the nearest whole number when above 0.5 and to the 1st decimal place when below.

Taxa Name	Mean annual abundance m^{-2} per site								Total mean biomass all sites (as g m^{-2})	Source of Length-Weight Equation	Taxa used in Original Equation
	1	2	3	4	5	6	7	8			
Dreissena rostriformis bugensis	0	0	68	130	40	37	41	7	**43.96**	Braungartber & Rothhaupt 2003	*Dreissena polymorpha*
Gammarus pulex	583	654	396	67	579	348	504	458	**14.34**	Marchant & Hynes 1981	*Gammarus pseudolimnaeus*
Ephemera danica	89	42	68	30	56	79	43	51	**8.06**	Huryn (Pers Comm. in Benke et al., 1999)	*Hexagenia limbata*
***Hydropsyche* spp.**	10	15	29	1	82	31	79	27	**3.01**	Smock 1980	*Hydropsyche* spp.
(Larvae) *Limnius volckmari*	72	12	63	5	112	118	109	56	**2.87**	Benke et al., 1999	Elmidae spp.
Theodoxus fluviatalis	3	1	21	0	7	20	37	31	**1.17**	Braungartber & Rothhaupt 2003	Gastropoda spp.
(Larvae) *Elmis aenea*	92	82	101	12	205	123	107	75	**1.04**	Benke et al., 1999	Elmidae spp.
Limnephilidae spp.	3	3	4	4	5	2	1	3	**1.01**	Huryn (Pers Comm. in Benke et al., 1999)	*Ironoquia parvula*
Baetis rhodani	22	67	34	3	138	67	92	118	**0.99**	Benke et al., 1999	*Baetis* spp.
***Simulium* spp.**	31	122	112	4	425	188	297	296	**0.88**	Huryn & Wallace 1987	Simuliidae spp.
Seratella ignita	147	77	23	2	52	39	54	28	**0.87**	Smock 1980	*Seratella* spp.
Calyopteryx splendens	0	3	2	2	1	1	2	3	**0.71**	Smock 1980	*Calopteryx spp.*
***Othocladiinae* spp.**	132	148	139	43	369	210	309	226	**0.46**	Smock 1980	*Orthocladiinae*
Bythinia tentaculata	3	4	4	4	6	4	2	9	**0.40**	Braungartber & Rothhaupt 2003	*B. tentaculata*
Erpobdella octoculata	0.2	1	0.5	1	1	0.5	0.5	1	**0.36**	Edwards et al., 2009	*Erpobdella octoculata*
***Chironomini* spp.**	49	28	32	24	26	21	11	33	**0.33**	Benke et al., 1999	*Chironomini*
Polycentropus flavomaculatus	11	19	6	2	3	5	4	4	**0.26**	Smock 1980	*Polycentropus* spp.
Ancylus fluviatalis	3	8	6	2	16	19	11	11	**0.23**	Braungartber & Rothhaupt 2003	Gastropoda spp.
(Larvae) *Gyrinus* spp.	3	1	2	0	5	1	0	1	**0.23**	Benke et al., 1999	Gyrinus spp.
***Oligochaeta* spp.**	62	102	70	89	47	64	53	50	**0.21**	Smock 1980	Oligochaeta spp.
Lymnea peregra	0	0	0	0	3	0	0	2	**0.19**	Braungartber & Rothhaupt 2003	*L. peregra*
Goera pilosa	1	1	0	0	5	1	1	1	**0.19**	Braungartber & Rothhaupt 2003	Trichoptera (cased)
***Tanypodinae* spp.**	17	18	23	24	32	21	15	21	**0.18**	Smock 1980	Tanypodinae spp.
Dreissena polymorpha	0	0	0	1	1	0	0	0	**0.18**	Braungartber & Rothhaupt 2003	*Dreissena polymorpha*
Asellus aquaticus	7	4	1	6	4	7	3	5	**0.17**	Braungartber & Rothhaupt 2003	*Asellus aquaticus*
Brachycentrus subnubilis	2	4	11	0	12	14	7	17	**0.16**	Smock 1980	*Brachycentrus* spp.
(Adult) *Elmis aenea*	40	32	24	1	74	17	25	59	**0.14**	Benke et al., 1999	Elmidae spp.
Sphaerium corneum	4	9	4	2	2	3	3	2	**0.13**	Smock 1980	*Pisidium* spp.
(Larvae) *Oulimnius* spp.	25	17	9	3	14	20	9	8	**0.12**	Benke et al., 1999	Elmidae spp.
Rhyacophila dorsalis	1	1	0	0	3	1	3	2	**0.12**	Benke et al., 1999	*Rhyacophila* spp.
Helobdella stagnalis	0	7	1	0	0	0	1	0	**0.10**	Edwards et al., 2009	*Glossiphonia complanata*
Athripsodes cinereus	4	3	2	1	5	2	3	4	**0.10**	Stoffels et al., 2003	*Oecetis spp.*
Glossiphonia complananta	0.3	2	0.2	0.2	0.2	0.2	0.2	0.2	**0.09**	Edwards et al., 2009	*Glossiphonia complanata*
Tinodes waerni	14	18	7	1	3	4	7	5	**0.09**	Braungartber & Rothhaupt 2003	*Tinodes waerni*
***Physidae* spp.**	0	0	0	0	0	0	0	2	**0.07**	Braungartber & Rothhaupt 2003	Gastropoda spp.
Heptagenia sulpheria	4	4	4	0	1	2	2	1	**0.07**	Benke et al., 1999	*Heptagenia* spp.
***Pisidium* spp.**	64	34	12	19	16	10	9	13	**0.06**	Smock 1980	*Pisidium* spp.
***Hydroptilla* spp.**	8	5	9	2	12	8	12	7	**0.06**	Braungartber & Rothhaupt 2003	*Hydroptilla sp.*
Caenis luctuosa	11	14	3	4	5	6	2	4	**0.06**	Smock 1980	*Caenis* spp.
Anisus vortex	0	0	1	0	0	1	0	1	**0.05**	Braungartber & Rothhaupt 2003	Gastropoda spp.
(Adult) *Limnius volckmari*	3	1	3	0	11	2	4	8	**0.05**	Benke et al., 1999	Elmidae spp.
Tipula spp.	0	0	0	0	1	0	0	0.3	**0.04**	Huryn & Wallace 1987	*Tipula abdomninalis*
Potamopyrgus antipodarum	0	0	0	1	0	0	3	1	**0.04**	Stoffels et al., 2003	*Potamopyrgus antipodarum*
Gyraulus albus	1	1	1	0	1	0	0	0	**0.03**	Braungartber & Rothhaupt 2003	Gastropoda spp.
***Tanytarsini* spp.**	14	17	15	9	15	14	13	25	**0.02**	Smock 1980	*Tanytarsini*
Molanna angustata	0	0	0	0	7	1	0	0	**0.02**	Braungartber & Rothhaupt 2003	*Tinodes waerni*
Sialis lutaria	0.2	1	0	1	0.3	0.3	0	0.3	**0.01**	Benke et al., 1999	Sialidae spp.
Bythinia leachii	0.3	0.2	0	0.2	0.5	0	0	0	**0.01**	Braungartber & Rothhaupt 2003	*B. tentaculata*
Denrocoelum lacteum	0	1	0	0	1	0	0	0	**0.01**	Benke et al., 1999	Tubellaria spp.
***Ceratopogonidae* spp.**	1	1	0.3	1	0	1	0.5	1	**0.01**	Benke et al., 1999	*Ceratopogonidae*
***Hydracarina* spp.**	1	1	0	0	1	1	2	1	**0.01**	Braungartber & Rothhaupt 2003	Hydracarina spp.
(Adult) *Oulimnius spp*	3	2	2	0	2	2	1	2	**0.01**	Benke et al., 1999	Elmidae spp.
Empididae spp.	0.2	0.3	0.3	0.0	0.2	0.5	0.2	0.0	**0.005**	Smock 1980	Empididae spp.
Crangonyx pseudogracilis	0	0	0	0	0	1	0	0	**0.003**	Benke et al., 1999	*Crangonyx gacilus*
Agapetus fuscipes	0	0	1	0	0	0	0	0	**0.002**	Benke et al., 1999	Glossosomatidae spp.
(Larvae) *Riolus* spp.	0	0	0	0	0	0	0	0	**0.002**	Benke et al., 1999	Elmidae spp.
Dugesia lugubris	0.2	0.5	0.2	0.2	0	0.5	0.5	0.2	**0.002**	Benke et al., 1999	Tubellaria spp.
Dugesia nigra/tenuis	0	0	0.2	0.3	0	0	0	0	**0.0002**	Benke et al., 1999	Tubellaria spp.
***Dicranota* spp.**	0	0	0	0	0	0.2	0	0	**0.0001**	Huryn & Wallace 1987	*Tipula abdomninalis*

Appendix II. Mean density of invertebrates (individuals m^{-2}) sampled on substrate tiles according to shell treatment category and experiment.

	Manipulated substrate tile deployment period and *D. r. bugensis* shell treatment														
	14 days					30 days					62 days				
Taxon	***Cont.* (0)**	**5 *shells***	**15 *shells***	**25 *shells***	**50 *shells***	***Cont.* (0)**	**5 *shells***	**15 *shells***	**25 *shells***	**50 *shells***	***Cont.* (0)**	**5 *shells***	**15 *shells***	**25 *shells***	**50 *shells***
Arthropoda															
Crustacea															
Isopoda															
Asellidae															
Asellus aquaticus	**0** ±0	**0** ±0	**0** ±0	**9** ±9	**0** ±0	**9** ±9	**0** ±0	**9** ±4	**0** ±0	**0** ±0	**0** ±0	**18** ±5	**9** ±9	**18** ±11	**18** ±18
Amphipoda															
Gammaridae															
Crangonyx pseudogracilis						**0** ±0	**0** ±0	**0** ±0	**231** ±103	**9** ±9					
Dikerogammarus haemobaphes						**0** ±0	**0** ±0	**9** ±4	**18** ±8	**27** ±18	**0** ±0	**0** ±0	**0** ±0	**27** ±27	**36** ±17
Gammarus pulex	**436** ±147	**622** ±58	**418** ±65	**560** ±83	**995** ±41	**684** ±142	**622** ±135	**827** ±81	**551** ±113	**2204** ±234	**631** ±146	**569** ±42	**613** ±137	**1022** ±76	**907** ±200
Insecta															
Coleoptera															
Elmidae															
Elmis aenea	**391** ±133	**560** ±138	**418** ±80	**382** ±84	**587** ±164	**302** ±121	**391** ±76	**436** ±43	**258** ±38	**489** ±136	**320** ±59	**240** ±28	**391** ±125	**409** ±98	**933** ±174
Limnius volkmarki	**124** ±53	**107** ±86	**151** ±75	**107** ±86	**124** ±60	**124** ±53	**204** ±75	**151** ±21	**36** ±13	**89** ±58	**142** ±81	**347** ±66	**356** ±92	**133** ±54	**231** ±96
Oulimnius spp	**27** ±18	**18** ±11	**36** ±17	**44** ±18	**71** ±52	**71** ±30	**98** ±29	**160** ±23	**169** ±46	**89** ±24	**62** ±27	**71** ±12	**98** ±38	**116** ±61	**169** ±71
Riolus spp.						**9** ±9	**9** ±9	**0** ±0	**0** ±0	**0** ±0					
Gyrinidae															
Gyrinus spp.	**0** ±0	**0** ±0	**0** ±0	**0** ±0	**9** ±9	**9** ±9	**0** ±0	**0** ±0	**9** ±4	**18** ±18	**0** ±0	**36** ±7	**18** ±11	**36** ±17	**36** ±26
Diptera															
Chironomidae															
Chironomini spp.	**0** ±0	**9** ±9	**18** ±11	**0** ±0	**9** ±9	**62** ±27	**44** ±20	**98** ±10	**44** ±11	**71** ±30	**0** ±0	**36** ±12	**9** ±9	**0** ±0	**0** ±0
Tanytarsini spp.	**0** ±0	**36** ±26	**36** ±26	**98** ±43	**98** ±49	**178** ±58	**98** ±59	**204** ±13	**213** ±34	**231** ±95	**9** ±9	**27** ±8	**44** ±20	**62** ±23	**116** ±39
Othocladiinae spp.	**160** ±36	**213** ±76	**276** ±86	**231** ±17	**480** ±244	**196** ±44	**240** ±44	**329** ±37	**302** ±63	**311** ±47	**44** ±14	**107** ±10	**36** ±17	**116** ±30	**462** ±87
Tanypodinae spp.	**44** ±28	**18** ±18	**62** ±27	**62** ±23	**89** ±47	**116** ±57	**133** ±31	**151** ±17	**187** ±35	**267** ±54	**27** ±11	**62** ±23	**27** ±18	**89** ±14	**178** ±28
Empididae															
Empididae spp.	**0** ±0	**9** ±9	**0** ±0	**0** ±0	**0** ±0										
Simuliidae															
Simulium spp.	**27** ±18	**36** ±17	**62** ±23	**9** ±9	**124** ±81	**0** ±0	**0** ±0	**0** ±0	**53** ±12	**27** ±27	**36** ±22	**27** ±5	**9** ±9	**9** ±9	**9** ±9
Ephemeroptera															
Baetidae															
Baetis rhodani	**27** ±18	**9** ±9	**9** ±9	**0** ±0	**0** ±0	**36** ±26	**36** ±17	**71** ±13	**80** ±13	**89** ±37	**0** ±0	**27** ±8	**0** ±0	**36** ±26	**62** ±33
Caenidae															
Caenis luctuosa	**53** ±17	**116** ±48	**142** ±47	**151** ±64	**142** ±38	**0** ±0	**44** ±24	**89** ±14	**53** ±12	**53** ±17	**213** ±45	**133** ±19	**240** ±46	**231** ±38	**382** ±116
Ephemerellidae															
Seratella ignita	**0** ±0	**9** ±9	**0** ±0	**0** ±0	**0** ±0	**0** ±0	**27** ±18	**18** ±5	**44** ±6	**116** ±46	**0** ±0	**0** ±0	**9** ±9	**0** ±0	**0** ±0

Appendix II. Continued.

	Manipulated substrate tile deployment period and *D. r. bugensis* shell treatment														
	14 days					30 days					62 days				
Taxon	***Cont.* (0)**	**5 *shells***	**15 *shells***	**25 *shells***	**50 *shells***	***Cont.* (0)**	**5 *shells***	**15 *shells***	**25 *shells***	**50 *shells***	***Cont.* (0)**	**5 *shells***	**15 *shells***	**25 *shells***	**50 *shells***
Ephemeridae															
Ephemera danica	**18** ± 18	**9** ± 9	**36** ± 17	**27** ± 27	**44** ± 34	**116** ± 62	**98** ± 43	**71** ± 12	**44** ± 11	**80** ± 33	**80** ± 36	**160** ± 23	**142** ± 17	**116** ± 33	**240** ± 105
Heptageniidae															
Heptagenia sulpheria	**0** ± 0	**18** ± 11	**9** ± 9	**0** ± 0	**18** ± 11	**9** ± 9	**0** ± 0	**0** ± 0	**0** ± 0	**0** ± 0	**0** ± 0	**0** ± 0	**0** ± 0	**0** ± 0	**0** ± 0
Tricoptera															
Brachycentridae															
Brachycentropus subnulis						**0** ± 0	**0** ± 0	**0** ± 0	**0** ± 0	**9** ± 9	**0** ± 0	**0** ± 0	**0** ± 0	**9** ± 9	**0** ± 0
Goeridae															
Goera pilosa						**0** ± 0	**9** ± 9	**0** ± 0	**0** ± 0	**0** ± 0	**0** ± 0	**0** ± 0	**9** ± 9	**9** ± 9	**9** ± 9
Hydropsychidae															
Hydropsyche spp.	**9** ± 9	**62** ± 30	**80** ± 17	**142** ± 38	**178** ± 44	**196** ± 46	**178** ± 96	**364** ± 19	**747** ± 116	**649** ± 170	**107** ± 33	**71** ± 10	**116** ± 36	**133** ± 40	**524** ± 246
Hydroptilidae															
Hydroptilla spp.	**0** ± 0	**0** ± 0	**0** ± 0	**9** ± 9	**9** ± 9	**27** ± 18	**53** ± 36	**231** ± 51	**142** ± 18	**107** ± 52	**0** ± 0	**0** ± 0	**0** ± 0	**0** ± 0	**0** ± 0
Leptoceridae															
Athripsodes cinereus	**36** ± 17	**18** ± 11	**9** ± 9	**44** ± 34	**9** ± 9	**27** ± 18	**27** ± 18	**27** ± 8	**9** ± 4	**27** ± 18	**36** ± 26	**62** ± 8	**89** ± 28	**62** ± 27	**107** ± 23
Limnephillidae															
Limnephillus lunatus						**0** ± 0	**0** ± 0	**0** ± 0	**9** ± 4	**0** ± 0					
Polycentropodidae															
Polycentropus flavomaculatus	**18** ± 11	**27** ± 27	**53** ± 17	**44** ± 14	**36** ± 17	**62** ± 27	**9** ± 9	**0** ± 0	**18** ± 8	**44** ± 34	**18** ± 11	**36** ± 7	**0** ± 0	**18** ± 18	**89** ± 37
Psychomidae															
Tinodes waerni	**9** ± 9	**44** ± 24	**0** ± 0	**9** ± 9	**9** ± 9	**0** ± 0	**0** ± 0	**27** ± 8	**0** ± 0	**0** ± 0	**0** ± 0	**18** ± 5	**0** ± 0	**9** ± 9	**18** ± 11
Zygoptera															
Calyoptegeridae															
Calyopteryx splendens	**0** ± 0	**0** ± 0	**18** ± 11	**0** ± 0	**18** ± 11	**0** ± 0	**0** ± 0	**18** ± 5	**9** ± 4	**0** ± 0	**0** ± 0	**0** ± 0	**0** ± 0	**0** ± 0	**27** ± 27
Arachnida															
Trombidiformes															
Hydracarina spp.						**0** ± 0	**0** ± 0	**0** ± 0	**0** ± 0	**9** ± 9	**0** ± 0	**0** ± 0	**0** ± 0	**0** ± 0	**27** ± 18
Clitellata															
Oligochaeta															
Oligochaeta spp.	**107** ± 65	**62** ± 27	**116** ± 30	**124** ± 33	**187** ± 51	**80** ± 38	**169** ± 86	**249** ± 29	**89** ± 14	**222** ± 81	**133** ± 42	**142** ± 26	**222** ± 49	**160** ± 48	**222** ± 66
Rhabditophora															
Triclada															
Dendroceolidae															
Dendrocoelum lacteum	**9** ± 9	**0** ± 0	**9** ± 9	**0** ± 0	**9** ± 9	**0** ± 0	**18** ± 11	**0** ± 0	**9** ± 4	**18** ± 18	**0** ± 0	**0** ± 0	**0** ± 0	**18** ± 18	**0** ± 0
Duguesidae															
Duguesia nigra/tenuis											**0** ± 0	**9** ± 4	**0** ± 0	**0** ± 0	**0** ± 0

Appendix II. Continued.

	Manipulated substrate tile deployment period and *D. r. bugensis* shell treatment														
	14 days					30 days					62 days				
Taxon	***Cont.* (0)**	**5 *shells***	**15 *shells***	**25 *shells***	**50 *shells***	***Cont.* (0)**	**5 *shells***	**15 *shells***	**25 *shells***	**50 *shells***	***Cont.* (0)**	**5 *shells***	**15 *shells***	**25 *shells***	**50 *shells***
Gastropoda															
Pulmonata															
Ancylidae															
Ancylus fluviatalis	**9** ±9	**9** ±9	**0** ±0	**0** ±0	**9** ±9	**18** ±18	**18** ±11	**0** ±0	**18** ±5	**18** ±18	**18** ±11	**0** ±0	**9** ±9	**0** ±0	**9** ±9
Planorbidae															
Anisus vortex	**0** ±0	**0** ±0	**9** ±9	**18** ±11	**0** ±0	**0** ±0	**0** ±0	**0** ±0	**0** ±0	**0** ±0	**0** ±0	**9** ±4	**0** ±0	**0** ±0	**0** ±0
Gyraulus albus	**9** ±9	**0** ±0	**0** ±0	**0** ±0	**0** ±0	**18** ±11	**0** ±0	**18** ±5	**18** ±5	**9** ±9	**0** ±0	**0** ±0	**18** ±11	**0** ±0	**9** ±9
Prosobranchia															
Bithyniidae															
Bythinia tentaculata	**0** ±0	**0** ±0	**0** ±0	**9** ±9	**9** ±9	**9** ±9	**0** ±0	**0** ±0	**0** ±0	**0** ±0	**0** ±0	**18** ±5	**18** ±18	**18** ±18	**0** ±0
Hydrobiidae															
Potamopyrgus antipodarum	**0** ±0	**0** ±0	**0** ±0	**9** ±9	**0** ±0	**9** ±9	**0** ±0	**0** ±0	**0** ±0	**0** ±0	**0** ±0	**0** ±0	**0** ±0	**9** ±9	**0** ±0
Lymnaeidae															
Radix peregra											**0** ±0	**0** ±0	**0** ±0	**0** ±0	**27** ±18
Hyrudinea															
Rhynchobdellida															
Erpobdellidae															
Erpobdella octoculata	**0** ±0	**27** ±27	**0** ±0	**9** ±9	**0** ±0	**0** ±0	**0** ±0	**0** ±0	**0** ±0	**9** ±9	**27** ±18	**18** ±8	**0** ±0	**18** ±11	**0** ±0
Glossiphonidae															
Glossiphonia complananta	**0** ±0	**0** ±0	**9** ±9	**0** ±0	**9** ±9	**0** ±0	**0** ±0	**0** ±0	**9** ±4	**9** ±9					
Helobdela stagnalis						**0** ±0	**0** ±0	**0** ±0	**0** ±0	**9** ±9	**0** ±0	**0** ±0	**0** ±0	**9** ±9	**0** ±0
Mollusca															
Bivalva															
Dreissenidae															
Dreissena bugensis	**0** ±0	**9** ±9	**0** ±0	**0** ±0	**9** ±9	**0** ±0	**0** ±0	**9** ±4	**27** ±5	**9** ±9	**36** ±17	**9** ±4	**44** ±34	**27** ±27	**18** ±11
Dreissena polymorpha						**0** ±0	**9** ±9	**0** ±0	**0** ±0	**0** ±0					
Sphaeriidae															
Pisidium spp.	**18** ±11	**18** ±18	**0** ±0	**9** ±9	**0** ±0	**53** ±17	**0** ±0	**62** ±17	**62** ±15	**98** ±26	**27** ±11	**71** ±8	**53** ±17	**27** ±18	**53** ±22
Sphaerium corneum						**0** ±0	**9** ±9	**9** ±4	**18** ±8	**0** ±0	**9** ±9	**0** ±0	**9** ±9	**0** ±0	**0** ±0
Total invertebrate density:	**1467** ±293	**2009** ±155	**1911** ±173	**2062** ±83	**3217** ±639	**2418** ±318	**2542** ±199	**3635** ±406	**3475** ±584	**5413** ±433	**1982** ±138	**2319** ±167	**2586** ±424	**2941** ±365	**4915** ±510

Appendix III. Mean density of invertebrate taxa (individuals m^{-2}) across littoral benthic sites in Barton Broad, Norfolk, UK, categorised by mean *D. polymorpha* density (individuals m^{-2}).

	Mean density individuals m^{-2} ± SE				
	Site group category by *D. polymorpha* denisty m				
Taxon	***Not Pres.***	**< 50**	**50-400**	**>400-800**	**>800**
Arthropoda					
Crustacea					
Arguloida					
Argulidae					
Argulus foliaceus	**0** ± 0	**0** ± 0	**1** ± 1	**0** ± 0	**0** ± 0
Isopoda					
Asellidae					
Asellus aquaticus	**0** ± 0	**4** ± 4	**7** ± 4	**0** ± 0	**60** ± 34
Amphipoda					
Corophidae					
Chelicorophium curvispinum	**1** ± 1	**15** ± 10	**2** ± 2	**65** ± 30	**135** ± 27
Gammaridae					
Dikerogammarus villosus	**6** ± 3	**88** ± 38	**102** ± 29	**509** ± 123	**451** ± 71
Insecta					
Anisoptera					
Libellulidae					
Sympetrum striolatum	**0** ± 0	**0** ± 0	**1** ± 1	**0** ± 0	**103** ± 40
Diptera					
Ceratopogonidae					
Ceratopogonidae spp.	**22** ± 7	**6** ± 5	**9** ± 5	**0** ± 0	**0** ± 0
Chironomidae					
Chironomidae spp.	**213** ± 28	**187** ± 47	**107** ± 19	**69** ± 40	**55** ± 20
Chaoboridae					
Chaoborus spp.	**1** ± 1	**0** ± 0	**0** ± 0	**0** ± 0	**135** ± 63
Hemiptera					
Corixidae					
Sigara spp.	**9** ± 3	**2** ± 2	**0** ± 0	**0** ± 0	**55** ± 27
Velidae					
Velia caprai	**1** ± 1	**0** ± 0	**0** ± 0	**0** ± 0	**287** ± 169
Megaloptera					
Sialidae					
Sialis lutaria	**0** ± 0	**4** ± 3	**0** ± 0	**0** ± 0	**37** ± 16
Tricoptera					
Limnephillidae					
Limnephillus lunatus	**0** ± 0	**0** ± 0	**0** ± 0	**4** ± 4	**92** ± 42
Phryganeidae					
Phryganea bipunctata	**3** ± 2	**2** ± 2	**0** ± 0	**0** ± 0	**103** ± 46
Clitellata					
Oligochaeta					
Oligochaeta spp.	**116** ± 17	**149** ± 19	**96** ± 6	**56** ± 17	**0** ± 0
Gastropoda					
Pulmonata					
Planorbidae					
Planorbis planorbis	**0** ± 0	**2** ± 2	**1** ± 1	**0** ± 0	**17** ± 8
Valvatidae					
Valvata piscinalis	**0** ± 0	**4** ± 3	**5** ± 3	**0** ± 0	**43** ± 7

Appendix III. Continued.

	Mean density individuals m^{-2} ± SE				
	Site group category by *D. polymorpha* denisty m				
Taxon	***Not Pres.***	**< 50**	**50-400**	**>400-800**	**>800**
Prosobranchia					
Bithyniidae					
Bythinia tentaculata	**1** ± 1	**2** ± 2	**6** ± 3	**9** ± 6	**0** ± 0
Hydrobiidae					
Potamopyrgus antipodarum	**0** ± 0	**24** ± 11	**0** ± 0	**34** ± 13	**0** ± 0
Lymnaeidae					
Lymnaea Stagnalis	**3** ± 2	**2** ± 2	**0** ± 0	**0** ± 0	**193** ± 105
Radix peregra	**9** ± 7	**6** ± 4	**15** ± 6	**4** ± 4	**0** ± 0
Neritidae					
Theodoxus fluviatalis	**0** ± 0	**0** ± 0	**0** ± 0	**0** ± 0	**72** ± 41
Physidae					
Physa spp.	**1** ± 1	**0** ± 0	**0** ± 0	**0** ± 0	**63** ± 26
Viviparidae					
Viviparus viviparus	**14** ± 10	**19** ± 8	**132** ± 31	**95** ± 29	**103** ± 19
Hirudinea					
Rhynchobdellida					
Erpobdellidae					
Erpobdella octoculata	**0** ± 0	**0** ± 0	**4** ± 3	**0** ± 0	**0** ± 0
Glossiphonidae					
Glossiphonia complananta	**0** ± 0	**0** ± 0	**0** ± 0	**4** ± 2	**0** ± 0
Mollusca					
Bivalva					
Dreissenidae					
Dreissena polymorpha	**0** ± 0	**15** ± 8	**193** ± 33	**685** ± 154	**1066** ± 179
Unionidae					
Anadonta anatina	**1** ± 1	**2** ± 2	**1** ± 1	**4** ± 4	**55** ± 37
Sphaeriidae					
Pisidium spp.	**0** ± 0	**17** ± 15	**0** ± 0	**0** ± 0	**60** ± 21
Miscilaneous					
Arachnida					
Acari					
Hydracarina spp.	**14** ± 2	**17** ± 7	**9** ± 5	**13** ± 19	**60** ± 31
Colembolla					
Colembolla spp.	**1** ± 1	**0** ± 0	**0** ± 0	**4** ± 4	**57** ± 35
Ostracoda					
Ostracoda spp.	**6** ± 3	**4** ± 4	**17** ± 6	**0** ± 0	**0** ± 0
Total density / *n* sites in category:	**422** ± 91	**571** ± 198	**708** ± 159	**1555** ± 449	**3302** ± 1064
***D. polymorpha* density / *n* sites:**	**0** ± 0	**15** ± 8	**193** ± 33	**685** ± 154	**1066** ± 179
***Dikerogammarus* density / *n* sites:**	**6** ± 3	**88** ± 38	**102** ± 29	**509** ± 123	**451** ± 71

Appendix IV. Environment Agency monitoring data by request for (1.) Wraysbury River 2015-2018 and (2.) Bartong Broad 2017-2018

Requests made via national enquiries email address: *enquiries@environment-agency.gov.uk*

1. *Wraysbury River Nr. Staines Moor (Lat: 51.448502, Long: -0.52494589)

Date Collected	Nitrate mg/L	Orthophosphate mg/L	Alkalinity as CaCO3 mg/L	Dissolved Oxygen mg/L	Alkalinity as CaCO3	Conductivity uS cm
12nd December 2015	**8.86**	**0.236**	**251**	**11.7**	**251**	**834**
1st June 2015	**11.1**	**0.336**	**222**	**9.91**	**222**	**850**
6th August 2015	**13.1**	**0.345**	**206**	**9.08**	**206**	**884**
13th November 2015	**10.8**	**0.332**	**221**	**8.95**	**221**	**897**
18th March 2016	**10.5**	**0.081**	**221**	**10.7**	**221**	**839**
23rd June 2016	**6.11**	**0.269**	**182**	**7.52**	**182**	**668**
15th September 2016	**12.2**	**0.345**	**234**	**8.18**	**234**	**882**
6th December 2016	**12.2**	**0.266**	**239**	**11**	**239**	**939**
19th January 2017	**10.2**	**0.246**	**222**	**11.5**	**222**	**886**
26th April 2017	**12.2**	**0.268**	**232**	**10.3**	**232**	**881**
28th March 2018	**9.87**	**0.214**	**210**	**11.1**	**210**	**1029**
13th April 2018	**7.24**	**0.178**	**221**	**10**	**221**	**873**
29th May 2018	**8.74**	**0.281**	**229**	**8.85**	**229**	**805**

Data in table above was collected by the **North East Thames Area Analysis and Reporting Team*

*DNM - **Recieved most recently updated data list on 2nd November 2018***

2. **Barton Broad, Norfolk Broads (Lat: 52.744918, Long: 1.4965436)

Date Collected	Nitrate mg/L	Orthophosphate mg/L	Alkalinity as CaCO3 mg/L
30th January 2017	**2.17**	**0.019**	**214**
23rd Febuary 2017	**2.05**	**0.01**	**209**
16th March 2017	**1.62**	**0.01**	**204**
26th April 2017	**0.196**	**0.01**	**170**
24th May 2017	**0.204**	**0.01**	**197**
20th June 2017	**0.196**	**0.01**	**194**
19th July 2017	**0.196**	**0.01**	**197**
15th August 2017	**0.195**	**0.01**	**184**
20th September 2017	**0.376**	**0.03**	**212**
18th October 2017	**0.363**	**0.01**	**224**
15th November 2017	**1.01**	**0.022**	**229**
11th December 2017	**1.41**	**0.02**	**206**
22nd January 2018	**1.81**	**0.025**	**182**
19th Febuary 2018	**2.14**	**0.012**	**185**
21st March 2018	**1.96**	**0.01**	**198**
20th April 2018	**1.2**	**0.01**	**202**
14th May 2018	**0.8**	**0.01**	**197**
15th June 2018	**0.196**	**0.01**	**201**

Data in table above was collected by the **East Anglia Area Analysis and Reporting Team*

*DNM - **Recieved most recently updated data list on 2nd November 2018***

RD2 Declaration (Previously known as the RD7)

Please email to researchdegrees@kcl.ac.uk along with your thesis submission

Student ID number	1154577
Student name	Daniel Nash Mills
Faculty	Global Affairs, Geography Department
Intended date of submission	21st December 2018
Word count of thesis	70562
Title of thesis	**ECOLOGICAL IMPACTS OF A NEW INVASIVE SPECIES IN UK RIVERS: THE QUAGGA MUSSEL, DREISSENA ROSTRIFORMIS BUGENSIS (BIVALVA: DREISSENIDAE; ANDRUSOV 1897)**

Has your thesis title changed since submission of the RD1: Yes ☐YES No ☐

Does your thesis include publications: Yes ☐YES No ☐

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DECLARATION:

I confirm that the following thesis does not exceed the word limit prescribed in the College regulations. I further confirm that the work presented in the thesis is my own and all references are cited accordingly.

Student signature	
Date	19th December 2018

Supervisor name	Michael A Chadwick
Supervisor signature	
Date	19th December 2018

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